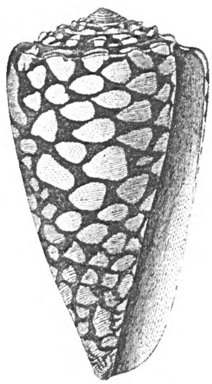

Molluscan Research

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The Malacological Society of Australasia

Molluscan Research

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Molluscan Research

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- The remainder of the manuscript should normally be arranged with the following components: **Abstract, Introduction, Materials and methods, Results, Discussion, Acknowledgments, References, tables, and table and figure captions** (but see sections below).
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- **Headings** for Introduction, Materials and methods, Results, Discussion, Acknowledgments and References should be in bold (in 12 pt) and on the left margin.

Short communications

This style of paper may be used to present the results of an important observation or well-designed but brief experiment in less than 6 manuscript pages. The paper must include a brief (up to 150 words) abstract and the Results and Discussion sections should be combined. The body of paper should be arranged in the following order: Introduction; Materials and methods; Results and discussion; Acknowledgments (if appropriate); References. No other headings may be used. The style for references, figures, tables, etc. is the same as for standard papers. Short papers introducing new taxa are also accepted (see 'New taxa' below).

Taxonomic papers

For taxonomic revisions, the same components (primary headings) as standard papers should be used (see above), but the following additional instructions apply.

- Headings for all taxonomic categories in taxonomic papers should be centred.
- Under each species or group taxon heading, list the sections and headings in the following order: Synonymies, including type details; Material examined (with subheadings: Type material; Other material); Diagnosis (optional); Description; Distribution; Remarks; Etymology.
- Authors' names and dates should be used for genus-group and species-group names used in headings. The abbreviations 'n. gen.', 'n. sp.', or 'n. subsp.' should be used for indicating a new genus, species, or subspecies.
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  Examples of format for species synonymy:
  Xus yus Smith, 1902: 304, pl. 3, fig. 4A; Jones, 1934: 456; Dick, 1956: 23, pl. 2, fig. 6. [Example of an available name.]
  Wus yus (Smith, 1902). Gail, 1978: 56, pl. 4, fig. 5. [Example where genus name has been changed.]
  Xus mus. – Hope, 1987: 21, pl. 3, fig. 8; Fred, 2000: 400 (not of Black, 1934). [Example of misidentification.]
  Example of format for genus synonymy:
  Xus Smith, 1902: 303. Type species (by subsequent designation of Jones, 1934: 456): *Xus yus* Smith, 1902; Recent, Bolivia.
  Wus Gail, 1978: 56. Type species (original designation): *Xus yus* Smith, 1902; Recent, Bolivia.
  - Multiple synonyms should be arranged in order of date of first application to the unit in question and, under each name, the separate references (if more than one is given) should be in chronological order.
  - If synonymies and references have previously been published these should not be repeated in full, if a reference to that source is given.
  - The type species, with author and date, should be cited immediately with the synonymy for each genus treated.
  - **Type data** should be given for each valid species treated, the museum in which the primary type (holotype, syntypes, lectotype or neotype) is preserved should be given or, if the whereabouts of the type are unknown, what steps were taken to ascertain its whereabouts. Designation of a lectotype must be accompanied by an express statement of the taxonomic purpose of the designation.
    Example of format for type data:
    Type data

    Holotype of *Condylocardia rectangularis*. Off Beachport, South Australia, 73 m (SAMA D.14979, ex. D.10113, 2 v). [Example where more than one type specimen.]
    Holotype. Off Emery Point, Darwin, Northern Territory, 12°27′S 130°49′E, coll. P. H. Colman, 25 Oct. 1969, on sandbar (AMS C.388191). [Example for new species.]
    Paratypes. Off Emery Point, Darwin, Northern Territory, 12°27′S 130°49′E, coll. P. H. Colman, 25 Oct. 1969, on sandbar (AMS C.379877, 8 v). Sandbar No. 1, Darwin, Northern Territory, 12°26′S 130°48′E, coll. O. J. Cameron, 14 Nov. 1970 (AMS C.379878, 4 v; NTM P14470, 1 v). [Example for new species.]
  - All types of new taxa must be lodged in a public museum. Authors should make every effort to ensure that types are lodged in the most appropriate institution in the region from which the species originates and in accordance with the requirements of collecting permits or legislation. Authors should be aware of the wildlife protection acts governing the import and export of specimens of wildlife in the countries in which specimens were collected.
- **Material examined.** Concise lists of specimens examined should be presented for each species.
  - For **type material**, reference should be made to the information presented under 'Type data'; where only some of the type material has been examined then registration numbers of specimens examined should be listed. Information for **non-type material** should be presented after the heading 'Other material' in the following format (items in [] are optional):
    Material examined

    Type material. See above. *Other material*. Locality, latitude and longitude, depth (if a marine species), [collector, date, habitat information], repository (i.e. museum), registered number (if available) (number of specimens – in parentheses). Locality, lat. long., etc.
  - Collection date should be given in the form 2 Aug. 2001.

  - For large material examined sections, authors should minimise the information to locality, repository, registered number and number of specimens only, and should summarise the information from label data in distribution maps or in the main text.
  - Records should normally be arranged geographically from north to south and east to west where practical.
  - Museum acronyms should conform to those normally used. They should be spelt out in a list under Materials and methods.
  - Museum registration numbers should be cited in the form required by the institution concerned, but there should never be a space between the letter and the number, i.e. C.3000 or F4000 not C 3000 or F 4000.
  - Citation of numbers of specimens should follow the registered number in the form (AMS C.3000, 2). You may wish to specify details such as separate valves, empty shells, etc.; this can be done using abbreviations, e.g. (AMS C.3000, 2 v, 1 c).
  - Use bold headings for country and state names, etc.
  - **Avoid needless repetition**: group common localities together in the following way:

    Sydney Harbour: Balmoral Beach, Lat. Long., date (museum registered number, number of specimens); Vaucluse, Lat. Long., date (museum registered number, number of specimens). Botany Bay: etc.

    Multiple lots from the same locality should be given in the following way:

    Balmoral Beach, Lat. Long.: date (museum registered number, number of specimens; museum registered number, number of specimens); date (museum registered number, number of specimens). Botany Bay, etc.
  - Summarise distributions in a **distribution map**.
  - Information regarding distribution, habitat, host association, seasonality, behaviour, and biology should be summarised in the body of the paper.
- **Diagnoses and descriptions**
  - The 'telegraphic' style is required for both.
  - Diagnoses should contain only the distinguishing characters or combination of characters for that taxon.
  - Descriptions should be subdivided by appropriate subordinate headings in italics at the left margin.
  - Comparative comments are to be placed under 'Remarks'.
  - The use of figures to illustrate descriptions is encouraged and should permit some reduction in the length of the verbal description of the parts figured.
- **Measurements.** Descriptions should be enhanced by the presentation of precise measurements of the type material and other relevant material in table format. All tables must be numbered (see Tables below). For shelled species, measurements of more than just length and width are encouraged.
- **Keys** should use clear-cut characters. The use of triplets, instead of couplets, is permissible to improve the efficiency of the key. Headings to keys should be self-explanatory. Tabular (i.e. synoptic or special purpose) keys are permitted where appropriate.

New taxa

It is recognised that there are a large number of new molluscan taxa to be described, particularly in the Indo-west Pacific region. This style of paper is intended for the introduction of one or a few new taxa where a comprehensive review or analysis of a group is not involved. The following sections must be used: Abstract; Introduction; Taxonomy; Discussion; Acknowledgments (if appropriate); References.

Each description of a new species-group taxon should contain the following subheadings in the order given: Name; Synonymy (if appropriate); Material examined (Type material and Other material); Diagnosis; Description (including a table of standard measurements); Remarks; Etymology. For genus-group taxa the following subheadings should be used in the order given: Name; Type species; Included species (list); Diagnosis; Remarks; Etymology.

The format for the text under each of the subheadings should be the same as in normal papers. The introduction to the paper should 'set the scene' and provide a brief overview of what is known about other related taxa (e.g. in the same genus). The description should be as comprehensive as possible and must include a table of standard measurements; in the remarks following the description, a comprehensive statement distinguishing the new taxon from related taxa should be given. The International Code of Zoological Nomenclature should always be adhered to. Primary type material must be lodged in a public

natural history museum. The discussion should include statements about the significance (e.g. biogeographic, evolutionary, conservation) of the new taxa or taxon.

General instructions

- **Statistical tests** should be described briefly and, if necessary, supported by references. Numbers of individuals, mean values, ranges and measures of variability should be stated. It should be made clear whether the standard deviation or the standard error of the mean has been given.
- The **International Code of Zoological Nomenclature** (Fourth Edition, effective from 1 January 2000) and decisions by the ICZN must be adhered to.
- **Tables** should be supplied in a separate file in a simple MS Word TABLE format without borders to columns and rows within the body of the table, apart from horizontal lines under the column headings. The width of tables (using 10 pt font) must not exceed the maximum width of the page (12.5 cm). Each table must be accompanied by a title. Normally data provided graphically should not be repeated in tabular form.
- **Footnotes** in the text are discouraged and should be used only when essential. They should be placed within horizontal rules immediately under the lines to which they refer.
- Latin names of genera and species and Latin words (*et al.*, *sensu lato*) should be in italics. Italics should not be used for any other purpose.
- The first mention in the text of the scientific name of a species or genus should be accompanied by the author and date, but subsequent use of these names should omit the author and date unless they are used in a heading.
- Numbers in the text should (unless given as actual units of measurement) be spelt out as words if less than 10 and as numerals if more than 10.
- Metric and Celsius units must be used. Do not give original imperial units unless quoting or for another particular reason.
- When citing distances and measurements insert a single space between the number and the dimension (e.g. 5 mm, not 5mm).

References

References should be cited in the text with the year of publication, e.g. Shepherd and Cannon (1988) or (Shepherd and Cannon 1988; Smith 1992, 1995). Note that commas are not used between the name and date in cited references. However, for authors of names, a comma should be included, as recommended in the International Code of Zoological Nomenclature. Two or more authors of a name should be linked by an ampersand (&).

Place a comma and a single space between the author's surname and first initial and one space between the initials (e.g. Smith, E. A.).

References must be listed alphabetically by first author and chronologically at the end of the paper in the form:

Journal article:

Shepherd, S. A., and Cannon, J. (1988). Studies on southern Australian abalone (genus *Haliotis*). X. Food and feeding of juveniles. *Journal of the Malacological Society of Australia* **9**, 21–26.

Note: titles of periodicals are italicised and must not be abbreviated. Only proper nouns are capitalised in the paper title.

Book:

Short, J. W., and Potter, D. G. (1987). 'Shells of Queensland and the Great Barrier Reef. Marine Gastropods.' (Golden Press: Drummoyne, Australia.)

Note: the book title is placed in quotes; nouns are capitalised in the book title; pagination should not be added.

Book chapter:

Kohn, A. J., and Amalsi, K. N. (1993). Comparative ecology of a biogeographically heterogeneous *Conus* assemblage. In 'The Marine Flora and Fauna of Rottnest Island, Western Australia'. (Eds F. E. Wells, D. I. Walker, H. Kirkman and R. Lethbridge.) pp. 523–538. (Western Australian Museum: Perth, Australia.)

Note: the book title is placed in quotes; only the first word and proper nouns are capitalised in the chapter title; all nouns are capitalised in the book title; pagination must be given only for the chapter.

Online reference:

Huelsenbeck, J. P., and Ronquist, F. (2001). 'MrBayes 2.01: Bayesian Inference of Phylogeny.' Available online at http://morphbank.ebc.uu.se/mrbayes/. [Accessed on 1 July 2003.]

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Figures must be submitted in final form, ready for publication. Electronic copies of figures are encouraged (see below).

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Effect of temperature and antibiotics on the hatching of *Microxeromagna armillata* (Mollusca : Hygromiidae) eggs: developing an *in vitro* bioassay for fungal egg parasites

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Abstract

Eggs of *Microxeromagna armillata* were incubated on water agar at different temperatures (5–40°C) and with each of three antibiotics (chloramphenicol, neomycin and streptomycin) at a range of concentrations (50–500 mg L^{-1}), to optimise conditions for a bioassay for egg parasites. Hatching of *M. armillata* progressed unimpaired over a wide temperature range (8–30°C). Delayed hatching occurred at 5°C and eggs died at temperatures of 37°C and above. Streptomycin had the least effect on hatching, with *M. armillata* tolerating concentrations up to 250 mg L^{-1}. Chloramphenicol and neomycin were inhibitory, even at concentrations of 50 mg L^{-1}.

Introduction

Microxeromagna armillata (Lowe, 1852) is a small terrestrial snail of Mediterranean origin (Hausdorf 1990) that has naturalised in Australia (Smith and Kershaw 1979). *Microxeromagna armillata* is of concern because it is considered quarantinable by some countries (Robinson 1999) and it is found as a contaminant of citrus fruit exports (Lush 1999). It is one of several introduced Mediterranean snails (viz. *Cernuella virgata* (daCosta, 1778), *Cochlicella acuta* (Müller, 1774), *Prietocella barbara* (Linnaeus, 1758) and *Theba pisana* (Müller, 1774)) that have become pests of agriculture, particularly in grain-production areas of southern Australia (Butler and Murphy 1977; Baker 1986; Baker *et al.* 1991). Consequently, these species are the subject of considerable research to understand their biology under local conditions and to find suitable methods for control.

Although biological control of pest snails has had some consideration in Australia (Hopkins and Baker 1993; Coupland and Baker 1995; Charwat and Davies 1999), no studies have examined fungal parasites of snail eggs. Fungal parasites of nematode eggs provide effective biocontrol in certain circumstances (Stirling 1991), so it is possible that snails could similarly be controlled by egg parasites. To evaluate the ability of fungi isolated from snail egg clusters to colonise eggs, it is necessary to establish a suitable bioassay. Because a supply of *M. armillata* eggs was available, this species was chosen for initial development of a bioassay. However, there was no information on conditions suitable for hatching *M. armillata* eggs, a necessary first step in developing a bioassay.

In initial attempts, bacterial growth around eggs of *M. armillata* incubated on water agar was inhibitory to fungal growth. Attempts to surface sterilise eggs of *M. armillata* with commonly used sterilants failed. Sodium hypochlorite (1%) rapidly dissolved the eggshell and diluted Hibitane (chlorhexidine gluconate 1% w/v, isopropyl alcohol 0.8%; ICI

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Pharmaceuticals, Melbourne, Australia) was absorbed, killing the snail. An alternative approach may be to control bacteria by inclusion of an antibiotic in the medium, provided it was not inhibitory to hatching. Therefore, the present study examined the effect of incubation temperature and exposure to antibiotics on the hatching of *M. armillata* eggs, with a view to selecting suitable conditions for the bioassay of fungal parasites.

Materials and methods

Source of snail eggs and hatching conditions

Pairs of laboratory reared *M. armillata* were enclosed in vented polycarbonate containers (200 mL, 70 mm diameter) with 150 mL field soil collected from Nangiloc, Victoria (34°28′21″S, 142°20′54″E) and several decaying citrus leaves. Snails were housed under a transparent waterproof cover in a shade house. Additional food (1:1:1 mix of rolled oats (Home Brand, Grocery Wholesalers, Sydney, Australia), skim milk powder (Diploma, Bonlac Food Supplies, Melbourne, Australia) and calcium carbonate (Univar, APS Finechem, Sydney, Australia)) was provided as required. Egg clusters were recovered at weekly intervals by sifting through the entire soil, which was then moistened and returned to the container. Eggs deposited were 0.9–1.2 mm in diameter, in clusters deposited up to 30 mm below the soil surface (A. L. Lush, unpublished observations). Clusters were stored individually on moist filter paper in the dark at 16°C for up to 7 days until used. At the time of collection, the eggs could be up to 1 week old. Therefore, immediately before use in the experiments, the egg clusters were suspended in sterile water and sorted under a dissecting microscope to select young eggs, with no obvious movement or shell development, before washing three times in sterile water.

Eggs were transferred aseptically to sterile water agar (1.5%; Sigma, St Louis, MO, USA) in 55-mm polystyrene Petri dishes and sealed in Parafilm (Pechiney Plastic Packaging, Menasha, WI, USA). Dishes contained five to eight equally spaced eggs. Eggs were examined daily for hatching and any hatchlings were removed to avoid consumption of unhatched eggs.

Effect of temperature and antibiotics on hatching

Three dishes of five eggs each were incubated at 5, 8, 16, 20, 26, 30, 37 and 42°C and examined daily for up to 5 weeks or until all eggs had hatched. From the data collected percent total hatch and mean days to hatch were calculated.

Filter (0.45-m)-sterilised solutions of streptomycin sulphate (Sigma), chloramphenicol (Sigma) and neomycin (Sigma) were added to molten water agar immediately before pouring plates to give final concentrations of 50, 125, 250 and 500 p.p.m. Fifteen eggs (five on each of three plates) were exposed to each concentration of streptomycin and sixteen eggs (eight on each of two plates) were exposed to each concentration of chloramphenicol and neomycin. Thirty-two eggs (eight on each of four plates) were included on unamended plates as controls. Plates were incubated at 16°C and observed daily for 8 days.

Statistical analysis

Analysis of variance was applied to the data using GENSTAT 5 (Lawes Agricultural Trust, Rothamsted Experimental Station, Harpenden, Hertfordshire, UK).

Results

Hatching occurred at temperatures of 30°C and below, with over 90% of eggs hatching, except at 5°C, at which temperature only 80% of eggs hatched. No hatching occurred at 37 and 42°C, although some embryo development was observed at 37°C in the first few days. The mean number of days to hatching (for those eggs that hatched) is presented in Fig. 1. There was no significant effect of temperature on the hatching rate between 16 and 30°C, but temperatures below 16°C reduced the hatching rate ($P < 0.001$).

The effects of antibiotics on hatching are presented in Fig. 2. Streptomycin had the least effect (Fig. 2*a*). At 500 mg L^{-1}, streptomycin delayed hatching (mean hatching time of 4.2 days per egg *v.* 2.1 days for control; $P = 0.05$) but, at this concentration, the reduction in percentage hatch from 80% to 60% was not significant. All concentrations of neomycin (Fig. 2*b*) delayed hatching (overall mean hatching time of 3.9 days; $P = 0.05$) and, at 500

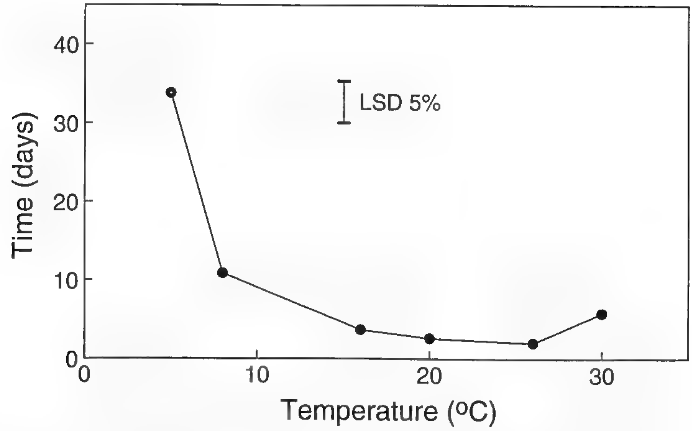

Fig. 1. Mean days to hatching for eggs of *Microxeromagna armillata* incubated on water agar over a range of temperatures (no hatch observed at temperatures of 37°C and above).

mg L^{-1} neomycin, the hatch was reduced to 14% ($P < 0.01$). Chloramphenicol (Fig. 2*c*), at concentrations of 125 and 250 mg L^{-1}, delayed hatching (mean hatching times of 6.3 and 4.6 days, respectively; $P = 0.05$). The mean percentage hatch was reduced to approximately 30% by 50–250 mg L^{-1} chloramphenicol, but 500 mg L^{-1} chloramphenicol had no effect (a significant quadratic effect; $P = 0.02$). All antibiotic treatments eliminated visible bacterial growth. Bacterial growth around eggs on control plates had no apparent effect on hatching.

Discussion

The present study has demonstrated that eggs of *M. armillata* will hatch on agar over a remarkably wide range of temperatures (8–30°C), with only minimal effect on development rate. This wide temperature tolerance of *M. armillata* eggs differs from *Helix aspersa* Müller, 1774 (Guéméne and Daguzan 1983) and many other invertebrates, where hatching has a relatively narrow optimal temperature range (in *H. aspera*, hatching occurred only at 20–25°C at 100% relative humidity). Because the eggs used were stored at 16°C for over 1 week before exposure to the various temperatures, this finding cannot be assumed to apply to eggs exposed immediately after deposition. Nevertheless, these data provide the flexibility to run a bioassay either at temperatures consistent with those experienced by eggs in the soil or at temperatures optimal for the fungi being assayed.

The three antibiotics assessed inhibit bacterial growth by binding to prokaryote rRNA, inhibiting protein synthesis (Corcoran and Hahn 1975), and successfully controlled bacterial contamination in our experiments. *Microxeromagna armillata* was least affected by streptomycin, but neomycin and chloramphenicol had clear detrimental effects. Chloramphenicol also causes mammalian toxicity through its inhibition of mitochondrial protein synthesis (Hardman and Limbird 2001), a phenomenon supporting the prokaryotic origin of mitochondria (Margulis 1981). Therefore, the effect of antibiotics that bind to prokaryotic ribosomes on molluscs is more likely to be direct toxicity, rather than by control of an essential symbiotic bacterial endophyte. Yao *et al.* (1993) also reported a molluscicidal effect of bacteriostatic antibiotics.

Incorporation of streptomycin in the medium at concentrations of 250 mg L^{-1} or less provides a suitable option for a bioassay. However, it may be possible to use more toxic

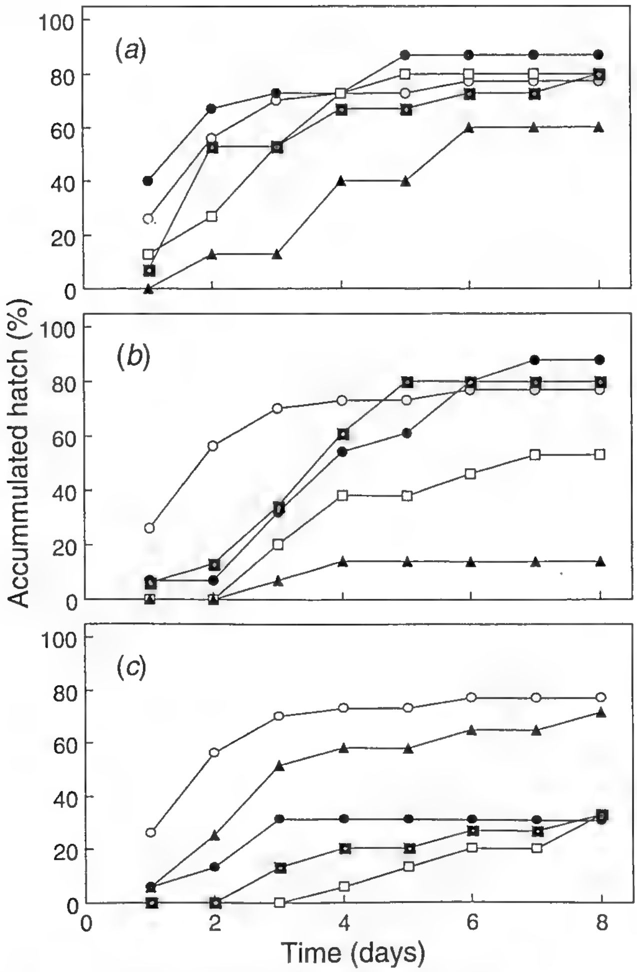

Fig. 2. Effect of (*a*) streptomycin sulphate, (*b*) neomycin and (*c*) chloramphenicol at concentrations of 0 (○), 50 (●), 125 (□), 250 (■) and 500 p.p.m. (▲) on the hatch of *Microxeromagna armillata* eggs.

antibiotics (such as neomycin, chloramphenicol or others) by only exposing the eggs briefly to these antibiotics. It is likely that streptomycin would be non-toxic to other snail species, but this would need confirmation.

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References

Baker, G. H. (1986). 'The Biology and Control of White Snails (Mollusca: Helicidae), Introduced Pests in Australia.' CSIRO Division of Entomology Technical Paper No. 25. (CSIRO Entomology: Canberra, Australia.)

Baker, G. H., Hawke, B. G., and Vogelzang, B. K. (1991). Life history and population dynamics of *Cochlicella acuta* (Müller) (Gastropoda: Helicidae) in pasture-cereal rotation. *The Journal of Molluscan Studies* **57**, 259–266.

Butler, A. J., and Murphy, C. (1977). Distribution of introduced land-snails of Yorke Peninsula, South Australia. *Transactions of the Royal Society of South Australia* **101**, 91–98.

Charwat, S. M., and Davies, K. A. (1999). Laboratory screening of nematodes isolated from South Australia for potential as biocontrol agents of helicid snails. *Journal of Invertebrate Pathology* **74**, 55–61. doi:10.1006/JIPA.1999.4855

Corcoran, J. W., and Hahn, F. E., Eds (1975). 'Antibiotics: Mechanism of Action of Antimicrobial and Antitumor Agents', Vol. 3. (Springer-Verlag: New York, USA.)

Coupland, J., and Baker, G. (1995). The potential of several species of terrestrial Sciomyzidae as biological control agents of pest helicid snails in Australia. *Crop Protection (Guildford, Surrey)* **14**, 573–576. doi:10.1016/0261-2194(95)00060-7

Guéméne, D., and Daguzan, J. (1983). Variations des capacités reproductrices de l'escargot «Petit-gris», *Helix aspersa* Müller (Mollusque Gastéeropode Pulmone Stylommatophore), selon son origine géeographique. II. Incubation des oeufs et éclosion de jenunes. *Annales de Zootechnie* **32**, 525–538.

Hardman, J. G., and Limbird, L. E., Eds (2001). 'Goodman & Gilman's The Pharmacological Basis of Therapeutics', 10th edn. (McGraw-Hill: New York, USA.)

Hausdorf, B. (1990). Über die verbreitung von *Microxeromagna armillata* (Lowe, 1852) and *Xerotricha conspurcata* (Draparnaud, 1801) in Greichenland und der Türkei. *Malakologische Abhandlugen Staatliches Museum für Tiekunde Dresden* **15**, 55–61.

Hopkins, D. C., and Baker, G. (1993). Biological control of white and conical snails. In 'Pest Control and Sustainable Agriculture'. (Eds S. A. Corey, D. J. Dall and W. M. Milne.) pp. 246–249. (CSIRO Publishing: Melbourne, Australia.)

Lush, A. L. (1999). Small brown snail control in citrus orchards. In 'Prime Notes', Version 9. (Queensland Department of Primary Industries: Brisbane, Australia.)

Margulis, L. (1981). 'Symbiosis in Cell Evolution: Life and its Environment on the Early Earth.' (W. H. Freeman: San Francisco, CA, USA.)

Robinson, D. G. (1999). Alien invasions: the effect of the global economy on non-marine gastropod introductions into the United States. *Malacologia* **41**, 413–438.

Smith, B. J., and Kershaw, R. C. (1979). 'Field Guide to the Non-marine Molluscs of South-eastern Australia.' (Australian National University Press: Canberra, Australia.)

Stirling, G. R. (1991) 'Biological Control of Plant Parasitic Nematodes.' (CAB International: Wallingford, UK.)

Yao, C., Hu, D., Shi, M., and Hu, G. (1993). Studies on antibiotic 230 as a molluscicide. *Japanese Journal of Medical Science and Biology* **46**, 103–119.

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New names for four common Marginellidae (Mollusca: Gastropoda) from northern New Zealand

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Abstract

The common littoral and shallow sublittoral New Zealand species hitherto identified as *Marginella pygmaea* Sowerby, 1846 and *M. mustelina* Angas, 1871, and a Kermadec Islands species similar to *M. mustelina*, are considered to be specifically distinct from Australian type material of these taxa. *Marginella pygmaea* is interpreted as a synonym of the Australian species *Mesoginella turbinata* (Sowerby, 1846) and the New Zealand species is described as new, together with a similar sympatric species. A New Zealand specimen is selected as neotype of *Marginella fasciata* Sowerby, 1846, which becomes the name for *M. mustelina* of authors, and the similar Kermadec Islands species is described as new.

Additional keywords: Australia, neotype, new taxa.

Introduction

The primary objective of the present contribution is to address doubts concerning the identity of two of the most common New Zealand littoral species, long known as *Marginella mustelina* A. Angas, 1871, and *M. pygmaea* Sowerby, 1846, which, it transpires, are both specifically distinct from their Australian type material. The opportunity is taken to describe a common new species of *Mesoginella* from the north-eastern North Island and a new species of *Serrata* from the Kermadec Islands. The only marginelloidean now known to be common to both Australia (New South Wales) and New Zealand (Raoul Island, Kermadec Islands) is the minute cystiscid *Pugnus parvus* Hedley, 1896 (Brook and Marshall 1998).

Twenty-eight species of Marginellidae are currently recognised in the New Zealand Recent fauna, although rich collections from there at Museum of New Zealand Te Papa Tongarewa contain well over twice this number (Marshall *et al.* in press).

Marginellids are carnivorous marine gastropods that occur worldwide at littoral to bathyal depths on soft and hard substrata. There are many hundreds of living species, and the family has a rich fossil record. In the latest revision (Coovert and Coovert 1995), the family was divided into two subfamilies, three tribes and 31 genera, and Cystiscidae was separated as a distinct family in Marginelloidea. Generic placements follow this revision, in which several taxa introduced by Laseron (1957) were newly synonymised. However, I favour the more conservative superfamilial classification of Ponder (1998*a*, 1998*b*).

Materials and methods

All New Zealand and Australian material at Museum of New Zealand Te Papa Tongarewa, Wellington (NMNZ) (registration numbers prefixed by 'M.') was examined, together with relevant type material at Auckland Institute and Museum, Auckland, and The Natural History Museum, London (BMNH). The height of the spire (i.e. the maximum measurable) was measured on the median shell axis from the tip of the protoconch to the suture on the last adult whorl, immediately behind the point at which the mature outer lip begins to thicken and climb adapically (expressed as a percentage of total shell height). Height precedes diameter in all given dimensions, and all measurements and radulae were taken from adult specimens.

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Protoconch whorl counting follows van Osselaer (1999; fig. 10). Radulae were cleaned with an aqueous solution of potassium hydroxide, sonicated and manipulated and mounted on double-sided adhesive carbon tabs. Images of shells and radulae (coated with carbon and gold/palladium) were captured by scanning electron microscope (SEM) and digital camera (uncoated shells). Unfortunately, live material was not available for description and illustration of living animals and comments on colour and colour pattern are derived from the literature and/or preserved specimens.

Systematics

Superfamily **MURICOIDEA** Rafinesque, 1815

Family **MARGINELLIDAE** Fleming, 1828

Subfamily **MARGINELLINAE** Fleming, 1828

Tribe **AUSTROGINELLINI** Coovert & Coovert, 1995

Genus ***Serrata*** Jousseaume, 1875

Serrata Jousseaume, 1875: 167. Type species (by tautonymy): *Marginella serrata* Gaskoin, 1849; Recent, Mauritius.

Haloginella Laseron, 1957: 284. Type species (by original designation): *Hyalina* (*Volvarina*) *mustelina* Angas, 1871; Recent, southern Australia.

Exiginella Laseron, 1957: 289. Type species (by original designation): *Marginella winteri* Tate, 1878; Middle Miocene, Victoria.

Diagnosis

Shell 3.6–13.0 mm long at maturity, white to brown, often banded, usually cylindrical; spire low to medium; outer lip thickened, finely to coarsely denticulate, rarely smooth; external varix present; no siphonal notch, parietal callus deposits or ridge; columella with four strong plications and with or without incipient adapical fifth plication, combined occupying less than half aperture length. Head simple, diverging cephalic tentacles slender, eyes set in expanded outer bases; siphon moderately long; mantle smooth or pustulose, extending over external shell surface. Radula uniserial, teeth 13–35, short and very broad, each with 22–59 cusps.

Remarks

Synonymy follows Coovert and Coovert (1995: 81), as does the diagnosis, which has been emended to include species/specimens (*S. fasciata*) that lack any trace of an adapical fifth columellar plication. Other New Zealand Recent species referrable to *Serrata*, in addition to the two recorded below, are *S. albescens* (Hutton, 1873), *S. maoriana* (Powell, 1932), *S. parvistriata* (Suter, 1908) and *S. plicatula* (Suter, 1910) (Spencer *et al.* 2002). Several additional (undescribed) species are known from the region (NMNZ).

Serrata fasciata (Sowerby, 1846)

(Figs 1*A*,*I*, 2*A*)

Marginella fasciata Sowerby, 1846: 389, pl. 76, fig. 142. – Weinkauff, 1879: 144, pl. 20, fig. 6; Tomlin, 1917: 266.

Volvarina rubrifasciata Jousseaume, 1875: 221. Unnecessary replacement name for *Marginella fasciata* Sowerby, 1846, which is not preoccupied by *Persicula fasciata* Martini, 1773 (not binomial) quoted in synonymy by Schumacher (1815: 235).

Marginella mustelina Suter, 1913: 460, pl. 20, fig. 13 (in part not Angas, 1871; New Zealand records only).

Marginella (*Volvarina*) *mustelina* Powell, 1932: 209 (in part; New Zealand records only).

Volvarina (*Haloginella*) *mustelina* Ponder, 1970: 56, 65, figs 1B,Ba,2H–L,3A,4A,Aa,G,Ga (not Angas).

Marginella (*Haloginella*) *mustelina* Powell, 1979: 218, fig. 49/1 (in part; New Zealand records only).

Haloginella mustelina Coovert, 1987*a*: 2, figs 1,2 (only). – Coovert, 1987*b*: 13 (in part; New Zealand records only); Coovert, 1989: 16, fig. 31 (in part; New Zealand records only).

Material examined

Neotype. (Here designated) NMNZ M.138250, Goat Island Bay, Leigh, New Zealand, alive, intertidal.

Other material examined. Three Kings Islands: King Bank, 33°57.4′S, 172°19.4′E, 128–123 m (4, M.138024); North West Bay, Great Island, alive, 12 m (2, M.117192); South East Bay, Great Island, 34°09.5′S, 172°08.8′E, alive, 20–22 m (5, M.134816); South East Bay, 34°09.5′S, 172°08.8′E, alive, 13–15 m (4, M.134896); off West Island, *Elingamite* wreck, 34°11′S, 172°03′E, 37 m (8, M.137879). Cape Maria van Diemen, beach (1, M.138025). Spirits Bay: W side of Pananehe Island, beach (4, M.59413); beach (1, M.17882). Doubtless Bay: N end Coopers Beach, alive under intertidal rocks (7, M.64303); Cooper's Beach (1, M.4707); Cable Bay, alive (6, M.17635; 4, M.16289). Hihi Beach, Mangonui Harbour, alive (3, M.49742). Reef Point, Ahipara, alive (3, M.90555). Cavalli Islands (4, M.6412). Tauranga Bay, Whangaroa: (2, M.90550; 7, M.6053). Bay of Islands: Tapeka, alive (12, M.90571; 30, M.4231); Russell, alive (7, M.9948). Poor Knights Islands: Northern Arch, Te Araara Point, 35°27′S, 174°44′E, 50 m (4, M.138018); Middle Arch, Tawhiti Rahi, 35°28′S, 174°44′E, 30 m (2, M.119457). Tutukaka, alive (5, M.37672). Ocean Beach, Whangarei Heads (4, M.90557). Goat Island Beach, Leigh: alive under stones resting on sand (12, M.8813; many, M.90573; 6, M.15607; 2, M.17719; 7, M.45635; 3, M.111117; 28, M.153789; 4, M.2980). Off NW tip of Little Barrier Island, 11–15 m (1, M.108925). Great Barrier Island: Oruawhero, alive (M.90570); Whangaparapara, alive under stones at low tide (15, M.4708). Howick, Auckland, alive (M.90565). Aldermen Islands, off E side of Ruamahua-nui Island, 36°57.2′S, 176°05.8′E, 38 m (3, M.112701). North Rock, Mount Maunganui, beach (1, M.64371). Boulder Bay, Motuhora Island, beach (4, M.44592). Off White Island: 37°30.5′S, 177°09.7′E, 64–69 m (5, M.137876); 37°30.5′S, 177°09.8′E, 62 m (5, M.119869); 37°30.6′S, 177°09.7′E, 73–59 m (30, M.94462); 37°30.6′S, 177°09.7′E, 64–69 m (9, M.137878). Motunui Rock, Omaio Bay, Cape Runaway, alive under intertidal rocks (many, M.39833). Te Kaha, alive (many, M.111979). Waihau Bay: Cemetary Point, beach and alive under intertidal rocks (many, M.153789; 4, M.44544); alive (many, M.15050; 2, M.9812); alive under rock slabs resting on mud (6, M.44545). Cape Runaway: 15–18 m (1, M.94156); Otamaroa, beach (1, M.113574). Lottin Point, alive (2, M.15102). Matakaoa Point, Hicks Bay (9, M.33172). Maruhou Point, Te Araroa, alive under intertidal rocks (1, M.58874). Ranfurly Bank, East Cape: 37°32.8′S, 178°48.7′E, 94 m (2, M.60758); 37°33.2′S, 178°50.3′E, 76–71 m (many, M.72658); 37°33.4′S, 178°48.3′E, 106–103 m (1, M.137877); 37°35.0′S, 178°51.6′E, 39–50 m (3, M.60883); 37°37.8′S, 178°52.4′E, 50–72 m (many, M.137875); 37°38.4′S, 178°51.7′E, 79–83 m (20, M.138027). Mahia Peninsula: beach (2, M.10093); Aurora Point, beach (1, M.138076).

Description

Shell 6.10–7.90 mm high and with 3.4–3.6 whorls at maturity, smooth, highly polished, narrowly ovate, height/width ratio 2.14–2.45 (mean 2.27; n = 12); spire short, conical, 8.2%–15.4% of shell height (mean 11.27; n = 12). Protoconch colourless, translucent, width of first half whorl 570–630 μm. Teleoconch translucent white with reddish brown bands, two subsutural rows of irregular maculations near insertion, another on adapical side of adapical columellar plait, and a broad, solidly pigmented band approximately midway between them; columellar plaits and mature outer lip white. Protoconch tip bluntly rounded, merging insensibly with teleoconch. Spire whorls flat; suture defined by fine line, not impressed; last adult whorl broadly and rather evenly convex, no anterior notch. Outer lip thickened at maturity, inner edge dentate, straight for most of its length or with slight, broad median indentation, broadly prosocyrt in profile. Columellar plaits strong, similar, plaited zone occupying approximately 42% of aperture length. Mantle smooth: other aspects of external and internal anatomy as described by Ponder (1970, under *Volvarina mustelina*). Radular teeth (Fig. 1*I*) very broad, subrectangular, with 33–37 small, sharp, narrowly conical, subequal cusps (four similar radulae examined by SEM).

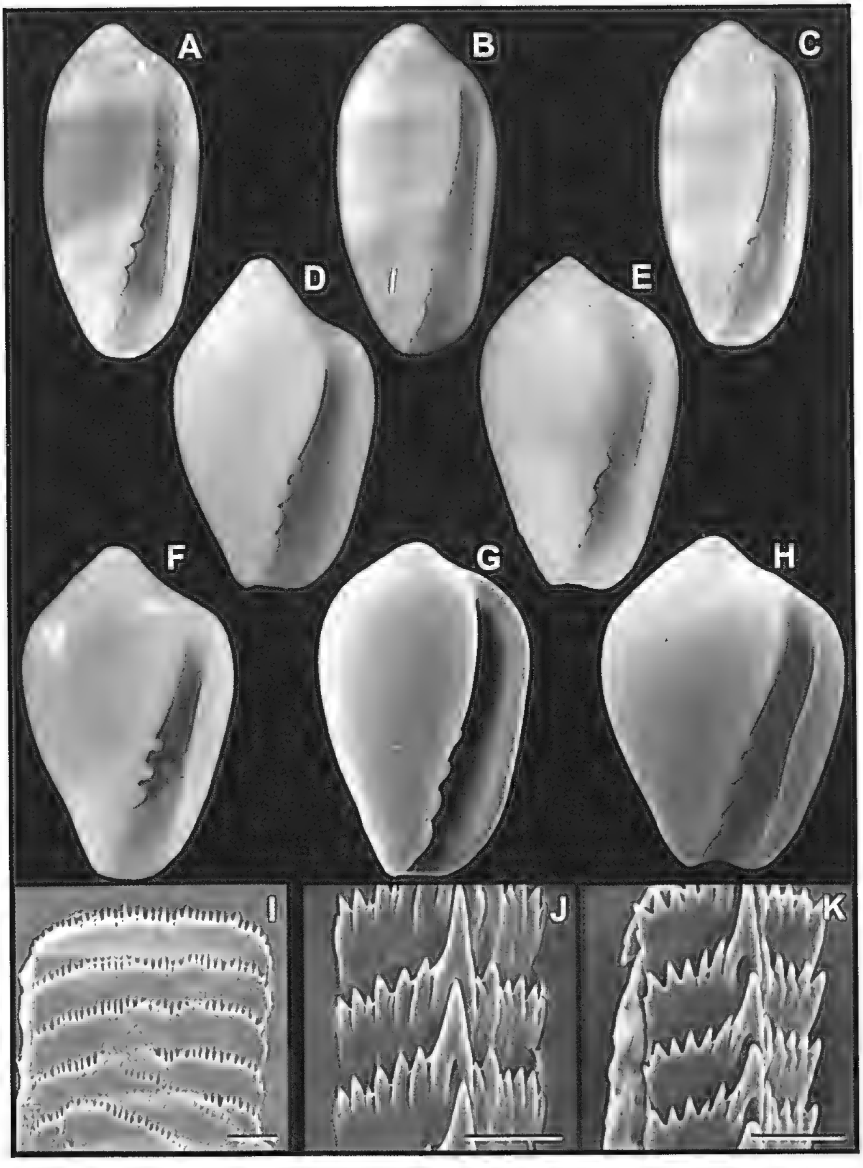

Fig. 1. Shells and radulae (*I–K*) of *Serrata* and *Mesoginella* species (G and H gold-plated for SEM, others natural). *A*, *Serrata fasciata* (Sowerby, 1846), neotype, Leigh, intertidal, 6.50 × 3.10 mm (M.138250). *B*, *Serrata raoulica* n. sp., holotype, Raoul Island, Kermadec Islands, 4.10 × 2.00 mm (M.272600). *C*, *Serrata mustelina* Angas, 1871, syntype, Port Jackson, New South Wales, 5.80 × 2.80 mm high (BMNH 1871.7.5.15). *D*, *Mesoginella koma* n. sp., holotype, Taurikura Bay, Whangarei Harbour, 5.20 × 2.98 mm (M.138047). *E*, *Mesoginella turbinata* (Sowerby, 1846) = holotype of *Marginella pygmaea* Sowerby, 1846 (BMNH 1880.9.18.7). *F*, *Mesoginella pisinna* n. sp., holotype, Matapouri Bay, 11–13 m, 4.60 × 3.00 mm (M.138251). *G*, *Mesoginella tryphenensis* (Powell, 1932), off Mayor Island, 59–74 m, 4.15 × 2.55 mm (M.66469). *H*, *Mesoginella pisinna*, paratype, Matapouri Bay, 11–13 m, 4.60 × 3.00 mm (M.134399). *I*, *Serrata fasciata*, Goat Island Beach, Leigh, intertidal (M.45635). *J*, *Mesoginella koma*, paratype, Taurikura Bay (M.23242). *K*, *Mesoginella pisinna*, paratype, Matapouri Bay, 11–13 m (M.134399). Scale bars = 20 μm.

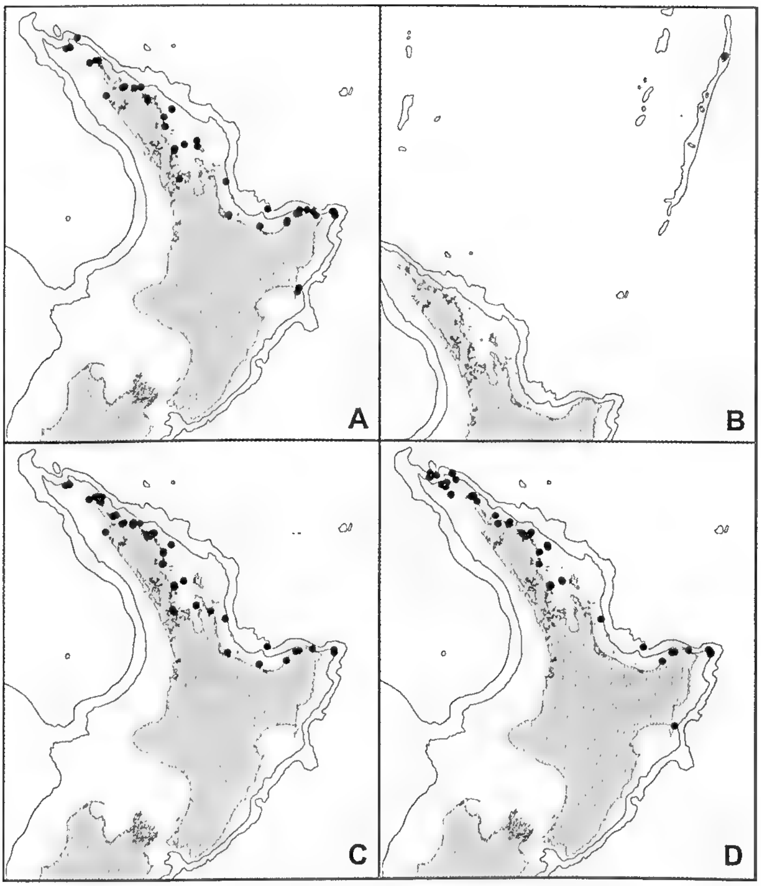

Fig. 2. Maps of northern New Zealand showing distributions of *Serrata* and *Mesoginella* species (200 and 1000 m isobaths indicated). *A*, *Serrata fasciata* (Sowerby, 1846). *B*, *Serrata raoulica* n. sp. *C*, *Mesoginella koma* n. sp. *D*, *Mesoginella pisinna* n. sp.

Distribution

Three Kings Islands, Cape Maria van Diemen to Spirits Bay, and north-eastern North Island as far south as Mahia Peninsula, New Zealand, 0–103 m; taken alive intertidally (under stones) to 22 m (Fig. 2*A*).

Remarks

The original description and illustration of *Marginella fasciata* (Sowerby 1846: 389, pl. 76, fig. 142) are accordant with both the Australian species *S. mustelina* (as suggested by Tomlin 1917: 266) and New Zealand specimens long so-identified. Because type material of *M. fasciata* is evidently no longer extant (not at BMNH: K. M. Way, personal communication, 2003), I select a New Zealand specimen as neotype, thus conserving Sowerby's taxon and providing a name for the New Zealand specimens, which are specifically distinct from *S. mustelina*. Weinkauff's (1879) illustration is presumably a crude copy of Sowerby's original. Jousseaume (1875) replaced *M. fasciata* with the name

Volvarina rubrifasciata, which, however, was unnecessary because Sowerby's name is not preoccupied (Tomlin 1917: 295).

Compared with syntypes (Fig. 1*C*) and other Australian specimens of *S. mustelina* (Ponder 1998, fig. 15.167C, as *mustellina* (sic)) (NMNZ) with adult facies in the same size range (height 6.5–7.0 mm), New Zealand specimens differ in having a more narrowly conical spire, a more evenly tapered base and in lacking an incipient adapical fifth columellar plait. New Zealand specimens differ further in having a pale yellowish brown instead of a deep reddish brown sutural line on the protoconch, in that the columellar plaits and adjacent base are white instead of reddish brown and in that the broad supramedian band is typically darker. The mantle is reportedly smooth in *S. fasciata* (Ponder 1970, fig. 1C), but papillate in *S. mustelina* (Hedley 1917: 709, pl. 50, fig. 3; Laseron 1957: 289, fig. 35).

Specimens from the Three Kings Islands (animal unknown) differ from North Island examples in being more darkly pigmented and in having a single solidly pigmented subsutural spiral band as wide as the two narrower rows of maculations of the mainland shells. Otherwise, they appear indistinguishable. Most specimens have a broad median colour band bounded by darker lines, but some North Island specimens are paler than usual and lack pigmentation between the bounding lines. The latter form is common between Te Kaha and Cape Runaway, especially at Waihau Bay, but rare elsewhere. There is complete gradation between weakly and strongly pigmented shells within populations.

Among other marginellids known from the New Zealand region (rich material NMNZ, including more than 30 undescribed species), *S. fasciata* is extremely distinctive in the combination of relatively large size (length up to 7.9 mm), brown colour and colour pattern. The north-eastern North Island species *S. maoria* (Powell, 1932) (several hundred specimens in 22 lots NMNZ), differs in details of colour pattern (Powell 1932), in attaining larger size (height up to 9.0 mm) and in having a toothless outer lip. The only other superficially similar species is described below.

Serrata fasciata has intracapsular, crawl-away development, with a single egg per capsule (Ponder 1970; Coovert 1986). Development of the other species discussed herein is unknown, but is likely to be direct also, because all have a paucispiral protoconch with a broad, bluntly rounded first whorl. It is scarcely suprising, therefore, that none of them is actually common to both Australia and New Zealand, as previous interpretations of *S. mustelina* and *Mesoginella pygmaea* suggested.

Serrata raoulica n. sp.

(Figs 1*B*, 2*B*)

Marginella mustelina Iredale, 1910: 71; Oliver. – 1915: 537 (not Angas, 1871).
Marginella (*Volvarina*) cf. *mustelina* Powell, 1932: 209, fig. 22 (not Angas).
Serrata sp. aff. *mustelina* Brook & Marshall, 1998: 226.

Material examined

Holotype. NMNZ M.272600, Raoul Island, Kermadec Islands, R. S. Bell.

Paratypes. Raoul Island, Kermadec Islands: R. S. Bell (16, NMNZ M.212468); dredged from gravel, 9–37 m (2, M.214612); W side of Meyer Island, 30 m (9, M.153930).

Other material examined. Raoul Island, Kermadec Islands: off W end of Napier Island, 40 m (11, M.153894).

Description

Shell 4.10–5.05 mm high at maturity, with 2.5–3.5 whorls, smooth, highly polished, narrowly ovate, height/width ratio 2.09–2.20 (mean 2.14; n = 6); spire short, conical,

13%–19% of shell height (mean 15.5%; $n = 6$). Protoconch translucent white, width of first half whorl 430–470 µm. Teleoconch translucent white, with pale orange–brown bands. Immature specimens with four narrow band with broader interspaces, one bordering suture, one above and beside adapical columella plait, others between them; with increasing shell size, bands broaden until considerably broader than interspaces, median two bands coalesce through pigmentation of interspace; adapical columellar plait pale buff, other plaits, area immediately outside them and mature outer lip white. Protoconch tip bluntly rounded, merging insensibly with teleoconch. Spire whorls flat; suture defined by fine line, not impressed; last adult whorl broadly and evenly convex, no anterior notch. Outer lip thickened at maturity, smooth, straight for most of its length or with slight, broad median indentation, broadly prosocyrt in profile. Columellar plaits strong, similar, plaited zone occupying approximately 46% of aperture length. Animal unknown.

Distribution

Raoul Island, Kermadec Islands, 30–40 m (shells only; Fig. 2*B*).

Remarks

The shell of *S. raoulica* differs principally from that of *S. fasciata* in attaining smaller size (height 5.05 *v.* 8.70 mm), in having a smaller protoconch (diameter of first half whorl 430–470 *v.* 570–630 µm), in having a broader abapical colour band and in that the adapical columellar plait shares the pigmentation of the (abapical) colour band outside it, unlike *S. fasciata*, in which all the plaits are white and the abapical colour band is on the adapical side of the adapical columella plait. It differs further from *S. fasciata*, and *S. mustelina* too, in having a smooth rather than dentate outer lip.

Etymology

From Raoul Island.

Genus ***Mesoginella*** Laseron, 1957

Mesoginella Laseron, 1957: 282. Type species (by original designation): *Marginella turbinata* Sowerby, 1846; Recent, south-eastern Australia.

Deviginella Laseron, 1957: 283. Type species (by original designation): *Marginella* (*Glabella*) *brachia* Watson, 1886; Recent, Queensland.

Hianoginella Laseron, 1957: 288. Type species (by original designation): *Marginella physa* Cotton, 1949; Pliocene, South Australia.

Sinuginella Laseron, 1957: 282. Type species (by original designation): *Marginella inconspicua* Sowerby, 1846; Recent, New South Wales.

Spiroginella Laseron, 1957: 283. Type species (by original designation): *Marginella leia* Cotton, 1944 = *Marginella turbinata* Sowerby, 1846; Recent, south-eastern Australia.

Urniginella Laseron, 1957: 287. Type species (by original designation): *Marginella cassidiformis* Tate, 1878; Middle Miocene, Victoria.

Diagnosis

Shell 2.5–11.0 mm long at maturity, glossy, smooth or with weak to distinct axial costae. White to yellowish–white, semi-opaque to translucent, rarely brownish–orange or with yellow bands. Narrowly to broadly obovate, obconic, biconic or broadly cylindrical, weakly to strongly shouldered. Spire of low to medium height with evenly contoured whorls; aperture moderately narrow; outer lip smooth to denticulate, moderately to strongly thickened, thickest medially; external varix present; weak siphonal notch present in most species; posterior notch weak to absent; ventral callusing usually absent; columella with

four strong plications occupying slightly less to slightly more than half aperture length, adapical plication remote in some species. Head simple, diverging cephalic tentacles slender, eyes set in their expanded outer bases; siphon long; mantle smooth or weakly pustulose, extending over external shell surface, foot narrow to broad. Radula uniserial, teeth 19–75, of moderate width, weakly arched, each with 9–22 strong cusps, central cusp typically strongest.

Remarks

Synonymy follows Coovert and Coovert (1995: 86), as does the diagnosis. Other New Zealand Recent species referrable to *Mesoginella*, in addition to the two recorded below, are *M. aupouria* (Powell, 1937), *M. cracens* (Dell, 1956), *M. ergastula* (Dell, 1953), *M. judithae* (Dell, 1956), *M. larochei* (Powell, 1932), *M. manawatawhia* (Powell, 1937), *M. otagoensis* (Dell, 1956), *M. pygmaeiformis* (Powell, 1937), *M. tryphenensis* (Powell, 1932) and *M. vailei* (Powell, 1932) (Spencer *et al.* 2002). There are, however, several additional species that remain to be described (NMNZ).

Mesoginella koma n. sp.

(Figs 1*D,E,J*, 2*C*)

Marginella pygmaea Suter, 1913: 465, pl. 20, fig. 19 (in part not Sowerby, 1846; New Zealand records only).

Marginella (*Glabella*) *pygmaea* Powell, 1932: 205, figs 18,20 (in part not Sowerby; New Zealand records only).

Volvarina (*Sinuginella*) *pygmaea* Coan, 1965: fig. 4 (not Sowerby).

Mesoginella (*Sinuginella*) *pygmaea* Ponder, 1970: 56, figs 1A,2A–G,4B,E (not Sowerby).

Marginella (*Sinuginella*) *pygmaea* Powell, 1979: 220, fig. 50/5 (not Sowerby).

Material examined

Holotype. NMNZ M.138047, between High Island and shore, Taurikura Bay, Whangarei Harbour, New Zealand, alive, 18 May 1961, W. F. Ponder.

Paratypes. Between High Island and shore, Taurikura Bay, Whangarei Harbour, alive (29, M.23242).

Other material examined. Off Three Kings Islands: 34°09.1′S, 172°08.4′E, North West Bay, Great Island, alive, 23 m (2, M.134675); 34°10′S, 172°08′E, 33 m (1, M.137972); off West Island, *Elingamite* wreck, 34°11′S, 172°03′E, 37 m (3, M.137964); South East Bay, Great Island, 15 m (3, M.117189). Cape Maria van Diemen, beach (3, M.138006). Pananehe Island, Spirits Bay: beach (9, M.5344; 4, M.8513; many, M.59395; 18, M.17881). Tom Bowling Bay (1, M.90546). Parengarenga Harbour: off Akatarere Point, 4 m (11, M.137967); Te Hapua, alive in intertidal pools in compacted mudstone platform beside wharf (11, M.49518); Te Hapua, alive, intertidal (22, M.42338). Reef Point, Ahipara (10, M.90564). Off Rangaunu Bay, 34°49.6′S, 173°15.0′E, 23 m (10, M.137957). Doubtless Bay: Cable Bay, beach (19, M.90569); Coopers Beach (1, M.138008); R.K. Dell (30, M.4232). Hihi Beach, Mangonui Harbour (1, M.21668). Bay in Stephensons Island, opposite Whangaroa Heads: 34°58′S, 173°47′E, 22–24 m (1, M.41338); 34°58′S, 173°47′E, 17–9 m (5, M.41539); beach (16, M.6051). Whangaroa: harbour entrance, main channel, 35°02′S, 173°45′E, 20 m (4, M.41098); centre of Kaouou Bay, 35°02′S, 173°45′E, 13 m (25, M.41805); Tauranga Bay (5, M.90572). Cavalli Islands, beach (5, M.6415). Bay of Islands: Deepwater Cove entrance, 35°12′S, 174°18′E, 33–46 m (1, M.138028); Deepwater Cove, 35°11.6′S, 174°18.1′E, 23–32 m (2, M.137963); 35°12.0′S, 174°16.3′E, 49 m (4, M.95747); Deepwater Cove (5, M.90551); Waewaetorea Passage, 35°12.4′S, 174°13.3′E, alive, 4 m (8, M.49334); Russell, beach (2, M.90558; 7, 112070); off Russell, 15 m (12, M.6050); 35°13.2′S, 174°17.4′E, 11–16 m (9, M.137966); Uruapukapuka Bay, 35°13.2′S, 174°14.3′E, 2–4 m (4, M.36088; 2, M.44344), 2 m (6, M.39734), 4 m (23, M.41244); Oke Bay, 35°13.4′S, 174°16.1′E, 3–5 m (4, M.96038); Bamboo Bay, Moturua Island, 35°13.9′S, 174°11.3′E, 4–6 m (13, M.44029); Orakawa Bay, 35°15.4′S, 174°12.2′E, 4–6 m (4, M.35617); near Knob Point, 35°15.4′S, 174°11.5′E, 4 m (7, M.44659); Manawara Bay, 35°15.7′S, 174°12.1′E, 2–6 m (1, M.40954); Paraoa Bay Point, 35°15.8′S, 174°10.4′E, 7 m (1, M.49415). S of Matapouri Bay, 35°34.8′S, 174°32.0′E, alive, 11–13 m (4, M.134398). Tutukaka, beach (17, M.90566). Whangarei Heads: beach (2, M.2974; 24,

M.90547); Taurikura Bay, alive, 2 m (4, M.138002; 13, M.42534); off Hat Island, 3 m (2, M.138009). Off NW tip of Little Barrier Island, alive, 11–15 m (4, M.108928). Leigh: beach (many, M.90576; 2, M.15606; 42, M.8822; 12, M.11116); off Panetiki Island, alive, 25 m (5, M.138022). Auckland: Cheltenham Beach (3, M.90549); Takapuna Reef (20, M.5083); Takapuna (many, M.90561); Campbell's Bay, beach (6, M.90574). Mercury Bay, Whitianga: (24, M.20584); alive (13, M.20583). Papaaroha, Coromandel, alive (4, M.90567). Off E side of Ruamahua-nui Island, Aldermen Islands, 36°57.2′S, 176°05.8′E, 38 m (1, M.137965). Mount Maunganui, beach (2, M.90548). Off Boulder Bay, Motuhora Island, alive, 11–13 m (8, M.44519); 18 m (1, M.44526). Off White Island, 37°30.6′S, 177°09.7′E, 64–69 m (10, M.137971). Motunui Rock, Omaio Bay, beach (50, M.33334). Otamaroa, Cape Runaway, beach (2, M.113575). Cemetary Point, Waihau Bay, beach (many, M.153706). Matakaoa Point, Hicks Bay, 37°34′S, 178°19′E (5, M.44623). Ranfurly Bank, East Cape: 37°35.0′S, 178°51.6′E, 39–50 m (1, M.137962); 37°38.4′S, 178°51.7′E, 79–83 m (1, M.137969).

Description

Shell 4.80–6.05 mm high at maturity, with 4.00–4.20 whorls, stout, smooth apart from minutely granulate parietal glaze, suture rather indistinct and defined by fine line, height/width ratio 1.60–1.82 (mean 1.68; $n = 12$), spire height 18.8%–23.7% of shell height (mean 21.8; $n = 12$). Protoconch translucent white, merging insensibly into teleoconch, width of first half whorl 470–450 µm. Teleoconch either translucent white, yellowish white, pale yellow or pale orange, some specimens with darker subsutural band. Spire conical, shoulder broadly rounded, spire whorls more or less flat. Outer lip strongly thickened at maturity, smooth. Anterior siphonal notch very shallowly indented. Columella plaits four, strong, zone occupied about half aperture length. Radular teeth (Fig. 1*J*) broad, broadly V-shaped, cusps narrowly conical, central cusp very long, flanked on each side by six or seven smaller, more or less subequal cusps (four similar radulae examined by SEM).

Distribution

Three Kings Islands, Cape Maria van Diemen eastwards, and north-eastern North Island as far south as East Cape, New Zealand, 0–83 m; taken alive intertidally to 25 m (Fig. 2*C*).

Remarks

Mesoginella koma is introduced for New Zealand *Marginella pygmaea* of authors not Sowerby, 1846.

Marginella pygmaea was based on a specimen without locality data, for which Powell (1932) 'provisionally' nominated New Zealand as type locality. However, comparison with the holotype (Fig. 1*G*) reveals that New Zealand specimens differ in attaining considerably smaller size (height of largest specimen examined 7.50 *v.* 8.50 mm). The holotype of *M. pygmaea* differs further from New Zealand specimens in having a low but distinct fasciole outside the adapical columella plait and in having five low, rounded axial costae on the shoulder of the last whorl: Coovert's (1999) contention that it is a New Zealand specimen is incorrect. The holotype of *M. pygmaea* is indistinguishable from weakly costate New South Wales forms of the common southern Australian species *Mesoginella turbinata* (Sowerby, 1846) (see Coovert 1988: 15), of which *M. pygmaea* is here considered to be a junior synonym (action here of the first reviser for taxa published simultaneously). The southern Australian species previously identified as *M. pygmaea* (May 1921, 1923) was renamed *M. pygmaeoides* by Singleton (1937) on the basis of differences between Tasmanian and New Zealand specimens reported by Powell (1932).

According to Tomlin (1917), the 'type' of *Marginella pymaea* was one of two specimens originally gummed to a tablet and was the 'larger of the two'. Sowerby (1846), however, stated that 'The specimen is in the collection of Mr Bell', so the second specimen must have

been added subsequently. Accordingly, it is concluded that the type specimen (BMNH 1880.9.18.7) is the holotype rather than a syntype as stated by Kaicher (1992: 6194).

This species was recorded (as *pygmaea*) from Foveaux Strait and the Chatham Islands by Suter (1913) and Powell (1932) on the basis of specimens from A. Hamilton's collection, dating from around the early 1900s. The provenance of much of Hamilton's material is extremely dubious, most notably that described by Murdoch (1905), reputedly from 'Whangaroa', which undoubtedly originated from Stewart Island or Foveaux Strait (Powell 1942: 125; Powell 1955: 62; Marshall 1978: 80). Because *M. koma* has not been obtained subsequently south of East Cape despite extensive shore collecting and dredging (NMNZ), there can be little doubt that Hamilton's material was mislocalised, a contention supported by the fact that the species was not recorded from the Chatham Islands by Finlay (1928), Dell (1960) or Marston (1996), and is not represented in extensive collections from Foveaux Strait (or Stewart Island) formed over several decades by E. C. Smith (NMNZ).

Mesoginella koma is the most common marginellid off mainland north-eastern North Island, both as beached shells and living intertidally to 25 m, where it is distinctive in the combination of smooth, white or yellowish shell, 5.00–7.50 mm high (adult facies), with a moderately elevated, conical spire. For the list of material examined, I have attempted to be conservative when interepretation of the limits of variation of this species, because it seems likely that some forms in the lower part of the bathymetric range may represent one or more additional distinct, although similar, species.

Etymology

Pallid (Maori).

Mesoginella pisinna n. sp.

(Figs 1*F,H,K*, 2*D*)

Mesoginella (*Sinuginella*) *tryphenensis* Ponder, 1970: 59 (not Powell 1932).

Material examined

Holotype. NMNZ M.138251, coast 1.6 km S of Matapouri Bay, Northland, New Zealand, 35°34.8′S, 174°32.0′E, alive, 11–13 m, 9 Feb. 1997, K. W. Burch, airlifted from steep rock face covered with red algae.

Paratypes. Coast 1.6 km S of Matapouri Bay, 35°34.8′S, 174°32.0′E, alive, 11–13 m (22, M.134399).

Other material examined. Off Three Kings Islands: Middlesex Bank, 33°57.0′S, 171°45.4′E, 98–103 m (35, M.137977); King Bank, 33°57.0′S, 172°19.0′E, 128 m (2, M.137993); King Bank, 33°57.4′S, 172°19.4′E, 128–123 m (15, M.137986); Middlesex Bank, 33°59.9′S, 171°45.3′E, 186–196 m (1, M.137983); Middlesex Bank, 34°01.2′S, 171°44.4′E, 206–211m (4, M.137978); Middlesex Bank, 34°02.0′S, 171°44.0′E, 246–291 m (2, M.138046); Middlesex Bank, 34°02.1′S, 171°45.8′E, 221–206 m (1, M.137973); 22 km ENE of Great Island, 34°05.0′S, 172°24.6′E, 200 m (2, M.137976); off North East Island, Great Island, 34°08.5′S, 172°11′E, 102 m (16, M.34513); off Prince's Rocks, 34°10′S, 172°08′E, 14 m (1, M.49804); North West Bay, Great Island, 34°09.1′S, 172°08.4′E, alive, 23 m (many, M.134674); South East Bay, Great Island, 34°09.5′S, 172°08.8′E, alive, 13–15 m (6, M.134897); South East Bay, 34°09.5′S, 172°08.8′E, alive, 20–22 m (42, M.134684); inner South East Bay, 34°10′S, 172°08′E, 27 m (1, M.137991); off N face of Hinemoa Island, 34°10.8′S, 172°02.6′E, 23 m (2, M.137982); S of Great Island, 34°14.1′S, 172°09.0′E, 192–202 m (2, M.137974); 28 km S of Great Island, 34°24.0′S, 172°16.8′E, 120 m (3, M.138033). Spirits Bay: beach (19, M.137995); W side of Pananehe Island, beach (16, M.137999). Off Akatarere Point, Parengarenga Harbour, 34°22′S, 173°03′E, 4 m (3, M.41305). Cable Bay, Doubtless Bay (6, M.137988). Matai Bay reef, Karikari Peninsula, 34°50′E, 173°25′S, 42 m (1, M.138021). Bay in Stephensons Island, opposite Whangaroa Heads: 34°58′S, 173°47′E, 22–24 m (7, M.41337); 34°58′S, 173°47′E, 17–9 m (2, M.41540). Immediately outside Whangaroa Harbour entrance, 35°00.35′S, 173°45.7′E, 25 m (3, M.137992). Bay of Islands: Deepwater Cove, 35°11.6′S, 174°18.1′E, 23–32 m (3, M.137989); near Knob Point, 35°15.4′S, 174°11.5′E, 4 m (1, M.44663); 35°10.5′S, 174°19.3′E, 36–53 m

(1, M.95681); between and N of Black Island and Moturoa, 35°12′S, 174°06′E, 31 m (3, M.41631); Oke Bay, 35°13.4′S, 174°16.1′E, 3–5 m (1, M.137987); Rawhiti Channel, 35°13.9′S, 174°15.5′E, alive, 3–5 m (9, M.95803); off Poroporo Island, 35°13.9′S, 174°13.1′E, alive, 6–7 m (1, M.43989). Poor Knights Islands: Northern Arch, Te Araara Point, 35°27′S, 174°44′E, 50 m (1, M.138015); Middle Arch, Tawhiti Rahi, 35°28′S, 174°44′E, 30 m (5, M.119466); South Harbour, Aorangi Island, 35°29′S, 174°44.5′E, alive, 25 m (3, M.138020); off The Pinnacles, 46 m (1, M.44718). Whangarei Heads: between High Island and shore, Taurikura Bay, alive (12, M.138023); Taurikura Bay, alive, 2 m (15, M.138003). Little Barrier Island: Waimaomao Bay, 36°10.5′S, 175°06.0′E, 10 m (1, M.138012); off Sugar Loaf, 36°10.7′S, 175°07.0′E, 24 m (2, M.138011). Leigh: North Reef, off NW tip of Goat Island, 18 m (2, M.49572); beach: (many, M.137960; 4, M.138044; 7, M.138040; 6, M.138039). Off Cape Rodney, 36°17.0′S, 174°49.5′E, alive, 20 m (5, M.138013). Off E side of Ruamahua-nui Island, Aldermen Islands: 36°57.2′S, 176°05.8′E, 38 m (3, M.112742); 36°57.3′S, 176°06.0′E, alive, 33 m (3, M.138010). Off White Island: 37°30.5′S, 177°09.7′E, 64–69 m (many, M.137994); 37°30.6′S, 177°09.7′E, 73–59 m (many, M.137990); 37°30.6′S, 177°09.7′E, 64–69 m (7, M.137996). Motunui Rock, Omaio Bay, beach (7, M.138043). Otamaroa, Cape Runaway, beach (15, M.138042). Cemetary Point, Waihau Bay, beach (many, M.137958). Matakaoa Point, Hicks Bay (4, M.138041). Ranfurly Bank, East Cape: 37°32.8′S, 178°48.7′E, 94 m (5, M.60756); 37°33.1′S, 178°49.5′E, 94–89 m (5, M.74685); 37°33.2′S, 178°50.3′E, alive, 76–71 m (many, M.72662); 37°35.0′S, 178°51.6′E, alive, 39–50 m (21, M.60882); 37°35.8′S, 178°52.7′E, 49 m (6, M.65459); 37°36.3′S, 178°53.1′E, 74 m (1, M.60923); 37°37.8′S, 178°52.4′E, 50–72 m (many, M.137997); 37°38.4′S, 178°51.7′E, 79–83 m (many, M.137998). Cemetary Point, Mahia Peninsula (2, M.138075).

Description

Shell 3.60–5.50 mm high at maturity, with 3.25–4.50 whorls, stout, broadly ovate, smooth apart from minutely granulate parietal glaze, suture rather indistinct and defined by fine line, height/width ratio 1.47–1.62 (mean 1.52; n = 14), spire height 14%–21% of shell height (mean 18.2; n = 14). Protoconch translucent white. Teleoconch uniform translucent white; or suture bounded by narrow white (adapical) and orange bands, base outside abapical three columella plicae and apertural rim opaque white, elsewhere pale translucent orange or buff, paler at periphery, or white. Protoconch bluntly rounded, merging insensibly into teleoconch. Spire broadly conical, shoulder broadly rounded, spire whorls more or less flat. Outer lip strongly thickened at maturity, smooth. Anterior siphonal notch very shallowly or not indented. Columella plaits four, strong, zone occupied about half aperture length. Radular teeth (Fig. 1*K*) broadly V-shaped, cusps sharp and narrowly conical, central cusp large, five or six smaller, subequal cusps on each side (five similar radulae examined by SEM).

Distribution

Three Kings Islands, Spirits Bay, and north-eastern North Island as far south as Mahia Peninsula, New Zealand, 0–291 m; taken alive at 2–76 m from rocky substrata with Bryozoa and shell (Fig. 2*D*).

Remarks

Compared with *Mesoginella koma*, *M. pisinna* differs in attaining smaller size (height of largest specimen seen 5.50 *v.* 7.50 mm) and in being smaller relative to the total number of whorls (shells with four whorls adult and approximately four mm high *v.* subadult and approximately five mm high). From examination of contracted, preserved, recently collected specimens taken together at the type locality of *M. pisinna*, *M. pisinna* differs further from *M. koma* by having darker, much more numerous pigmentation spots. In comparing living specimens taken together at Whangarei Heads, Ponder (1970) observed that living specimens of *M. pisinna* (as *M. tryphenensis* Powell) differed from *M. koma* (as *M. pygmaea*) by having more dark pigmentation and the yellow pustules on the mantle more

distinctly raised. *Mesoginella koma* occurs throughout most of the geographic range of *M. pisinna* and is uncommon deeper than 20 m, whereas *M. pisinna* ranges deeper and is common from approximately 2–80 m on appropriate substrata. As with *M. koma*, for the list of material examined, interpretation of the limits of variation of this species is conservative, because it seems likely that some forms in the lower part of the bathymetric range represent several additional distinct, but similar, species.

Compared with *M. aupouria* (Powell, 1937), adults of which may be of equivalent size, although usually larger, *M. pisinna* differs by having a higher, more narrowly conical spire and a considerably thinner outer lip at maturity. *Mesoginella aupouria* is known only from off the Three Kings Islands at 100–805 m (11 lots NMNZ; holotype BMNH 19621061). The sympatric (but asyntopic) species *M. tryphenensis* (Powell, 1932) is more superficially similar, being narrower, consistently white, with a shorter spire, a smaller protoconch and a weak but distinct fasciole outside the adapical second columellar plait (Fig. 1*G*).

During the present study, specimens of *M. pisinna* and *M. koma* were found mixed together in many samples identified as *M. pygmaea*, and the two species have been taken living together at several localities at 2–13 m depth.

Etymology

Small (Latin).

Discussion

The recognition of different species on opposite sides of the Tasman Sea is not surprising given that endemism among New Zealand molluscs is extremely high, more than 86% of recorded marine species being endemics (Spencer *et al.* in press). This is particularly likely in taxa having direct development. *Serrata fasciata* has intracapsular, crawl-away development, with a single egg per capsule (Ponder 1970; Coovert 1986). Although development of the other species discussed here is unknown, it seems likely to be direct also, because all have a paucispiral protoconch with a broad, bluntly rounded first whorl. It is scarcely surprising, therefore, that none of them is actually common to both Australia and New Zealand, as previous interpretations of *S. mustelina* and *Mesoginella pygmaea* suggested. The only marginelloidean now known to occur on both sides of the Tasman Sea is the minute cystiscid *Pugnus parvus* Hedley, 1896 (New South Wales and Kermadec Islands; Brook and Marshall 1998).

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References

Brook, F. J., and Marshall, B. A. (1998). Checklist of benthic coastal marine Mollusca from the northern Kermadec Islands. Appendix, pp. 210–233 *in* Brook, F. J. The coastal molluscan fauna of northern Kermadec Islands, southwest Pacific Ocean. *Journal of the Royal Society of New Zealand* **28**, 185–233.

Coan, E. (1965). A proposed reclassification of the family Marginellidae. *The Veliger* **7**, 184–194.

Coovert, G. A. (1986). A review of marginellid egg capsules. *Marginella Marginalia* **1**, 13–19.

Coovert, G. A. (1987*a*). Proper useage of the generic names *Haloginella, Hyalina*, and *Volvarina* with a diagnosis of the genus *Haloginella*. *Marginella Marginalia* **3**, 1–7.

Coovert, G. A. (1987*b*). A literature review and summary of marginellid external anatomy. *Marginella Marginalia* **3**, 8–25.

Coovert, G. A. (1988). Type species of the genera *Austroginella* and *Mesoginella* and their synonyms. *Marginella Marginalia* **4**, 9–26.

Coovert, G. A. (1999). Revision of the nomenclature of the Kaicher *Marginella* card packs (Cystiscidae, Marginellidae). *Marginella Marginalia* **10**, 1–39.

Coovert, G. A., and Coovert, H. K. (1995). Revision of the supraspecific classification of marginelliform gastropods. *The Nautilus* **109**, 43–110.

Dell, R. K. (1960). Chatham Islands marine Mollusca based on collections of the Chatham Islands Expedition, 1954. Biological Results of the Chatham Islands 1954 Expedition 4. *New Zealand Department of Scientific and Industrial Research Bulletin* **139**, 141–157.

Finlay, H. J. (1928). The Recent Mollusca of the Chatham Islands. *Transactions of the New Zealand Institute* **59**, 232–286.

Hedley, C. (1917). Studies on Australian Mollusca. Part 13. *Proceedings of the Linnean Society of New South Wales* **41**, 680–719.

Iredale, T. (1910). On marine Mollusca from the Kermadec Islands, and on the 'sinusigera apex'. *Proceedings of the Malacological Society of London* **9**, 68–79.

Jousseaume, F. P. (1875). Coquilles de la famille des marginelles. Monographie. *Revue et Magasin de Zoologie Pure et Appliquée* **3**, 164–271, 429–435.

Kaicher, S. D. (1992). Marginellidae. Part 3. In 'Card Catalogue of World-Wide Shells.' Pack 60. (Kaicher: St Petersburg, FL, USA.)

Laseron, C. F. (1957). A new classification of the Australian Marginellidae (Mollusca), with a review of species from the Solanderian and Dampierian zoogeographical provinces. *Australian Journal of Marine and Freshwater Research* **8**, 274–311.

Marshall, B. A. (1978). Cerithiopsidae (Mollusca: Gastropoda) of New Zealand, and a provisional classification of the family. *New Zealand Journal of Zoology* **5**, 47–120.

Marshall, B. A., Spencer, H. G., and Willan, R. C. (in press). Recent Mollusca. In 'The New Zealand Inventory of Biodiversity: A Species 2000 Symposium Review.' (Ed. D. P. Gordon.) (Canterbury University Press: Christchurch, New Zealand.)

Marston, J. (1996). The molluscs of the Chatham Islands:1994. *Cookia. Journal of the Wellington Shell Club* **7**, 15–56.

May, W. L. (1921). 'Checklist of the Mollusca of Tasmania.' (Vail, Government Printer: Hobart, Australia.)

May, W. L. (1923). 'An Illustrated Index of Tasmanian Shells. With 47 Plates and 1052 Species.' (Vail, Government Printer: Hobart, Australia.)

Murdoch, R. (1905). Additions to the marine Mollusca of New Zealand. *Transactions of the New Zealand Institute* **37**, 217–232.

Oliver, W. R. B. (1915). The Mollusca of the Kermadec Islands. *Transactions of the New Zealand Institute* **47**, 509–568.

Ponder, W. F. (1970). Some aspects of the morphology of four species of the neogastropod family Marginellidae with a discussion on the evolution of the toxoglossan poison gland. *Journal of the Malacological Society of Australia* **2**, 55–81.

Ponder, W. F. (1998*a*). Superfamily Muricoidea. In 'Mollusca: The Southern Synthesis. Fauna of Australia 5. Part B'. (Eds P. L. Beesley, G. J. B. Ross and A. Wells.) pp. 819–820. (CSIRO Publishing: Melbourne, Australia.)

Ponder, W. F. (1998*b*). Family Marginellidae. In 'Mollusca: The Southern Synthesis. Fauna of Australia 5. Part B'. (Eds P. L. Beesley, G. J. B. Ross and A. Wells.) pp. 838–841. (CSIRO Publishing: Melbourne, Australia.)

Powell, A. W. B. (1932). The Recent Marginellidae of New Zealand, with descriptions of some new species. *Transactions of the New Zealand Institute* **62**, 203–214.

Powell, A. W. B. (1942). The New Zealand Recent and fossil Mollusca of the family Turridae. *Bulletin of the Auckland Institute and Museum* **2**, 1–188.

Powell, A. W. B. (1955). 'Mollusca of the Southern Islands of New Zealand. Cape Expedition Series Bulletin 15.' (Department of Scientific and Industrial Research: Wellington, New Zealand.)

Powell, A. W. B. (1979). 'New Zealand Mollusca. Marine, Land and Freshwater Shells.' (Collins: Auckland, New Zealand.)

Schumacher, C. F. (1817). 'Essai d'un nouveau système des habitations des vers testaces avec XXII planches.' (Schultz: Copenhagen, Denmark.)

Singleton, F. A. (1937). Mollusca. Lady Julia Percy Island 1935 Expedition. *Proceedings of the Royal Society of Victoria* **49**, 387–396.

Sowerby, G. B. (2nd of name) (1846). Monograph of the genus *Marginella.* In 'Thesaurus Conchyliorum, or Monographs of Genera of Shells' 1 (7). pp. 373–406. (Sowerby: London, UK.)

Spencer, H. G., Willan, R. C., and Marshall, B. A. Murray, T.J. (2002). 'Checklist of the Recent Mollusca described from the New Zealand Exclusive Economic Zone.' http://toroa.otago.ac.nz/pubs/spencer/Molluscs/index.html [Accessed March 2004]

Spencer, H. G., Marshall, B. A., Maxwell, P. A., Grant-Mackie, J. A., Stilwell, J. D., Campbell, H. J., Willan, R. C., and Crampton, J. S. (in press). Phylum Mollusca. Chitons, clams, snails, slugs, squids and octopuses. In 'The New Zealand Inventory of Biodiversity: A Species 2000 Symposium Review.' (Ed. D. P. Gordon.) (Canterbury University Press: Christchurch, New Zealand.)

Suter, H. (1913). 'Manual of the New Zealand Mollusca, with an Atlas (1915) of quarto plates'. (Mackay, Government Printer: Wellington, New Zealand.)

Tomlin, J. R. LeB. (1917). A systematic list of the Marginellidae. *Proceedings of the Malacological Society of London* **12**, 242–306.

van Osselaer, C. (1999). Counting shell whorls. Remarks. *Apex* **14**, 33–42.

Weinkauff, H. C. (1878–1879). Die Gattungen *Marginella* und *Erato*. 'Systematisches Conchylien Cabinet von Martini und Chemnitz. Vol. 5, Part 1.' (Bauer & Raspe: Nürnberg, Germany.)

CSIRO PUBLISHING

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Mineralisation in the teeth of the limpets *Patelloida alticostata* and *Scutellastra laticostata* (Mollusca : Patellogastropoda)

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Abstract

The sequence and ultimate pattern of mineralisation in the major lateral radula teeth of two species of limpet, namely *Patelloida alticostata* and *Scutellastra laticostata* (Mollusca : Patellogastropoda), have been elucidated using energy dispersive, Raman and infrared spectroscopies. In both species, iron is the first element infiltrated into the teeth and, in the form of goethite, occupies the posterior cutting surface of the tooth cusps, whereas silica mineralises the rest of the tooth. The first onset of mineralisation, as judged by the initial influx of iron, occurs in the junction zone, the region separating the tooth cusp from the tooth base. Although differences between the two species do exist, the general pattern of tooth mineralisation is very similar, suggesting that the mineralisation of iron and silica is a very ancient character, both in this group and among molluscs as a whole.

Additional keywords: biomineralisation, goethite, iron, mollusc, silica.

Introduction

Molluscan teeth have long been a source of investigation and inspiration for biologists and chemists alike owing to the presence, in many species, of bioinorganic deposits (Lowenstam and Weiner 1989). These deposits, or biominerals as they are known and which are used to strengthen the teeth, range from the widespread hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$) found in the teeth of many molluscan groups, to magnetite (Fe_3O_4), which is found only in chitons (Lowenstam 1962*a*; Kim *et al.* 1989; Macey and Brooker 1996). One of the more widespread molluscan groups is the limpets (order Patellogastropoda), which are common in the intertidal region throughout the world. In the limpets, as well as organic components, the major lateral teeth can contain up to 12% ferric oxide, chiefly as goethite (α-FeOOH), 7%–16% silica in the form of hydrated amorphous opal ($SiO_2.nH_2O$) and small amounts of calcium (Jones *et al.* 1935; Lowenstam 1962*b*; Runham *et al.* 1969; Grime *et al.* 1985; Burford *et al.* 1986; Mann *et al.* 1986; Lu *et al.* 1995). In limpets, as in most molluscs, the teeth are arranged in rows along a tongue-like organ, the radula. Because teeth at the mature end of the radula are lost continually by wear and breakage during feeding, they need to be replaced and, thus, the radula is composed of a sequence of teeth in various stages of mineralisation (Runham and Thornton 1967; Mann *et al.* 1986). Although several studies of the mineralisation of limpet teeth have been undertaken, they have been limited, in the main, to either bulked samples or individual teeth from which the various components have been extracted (see, for example, Mann *et al.* 1986). Recent advances in techniques now permit a detailed analysis to be conducted of the mineralisation process *in situ*, allowing a description to be given of both the process of mineralisation and the nature of the materials involved. The two limpet species investigated in the present study, namely *Patelloida alticostata* and *Scutellastra laticostata* (previously

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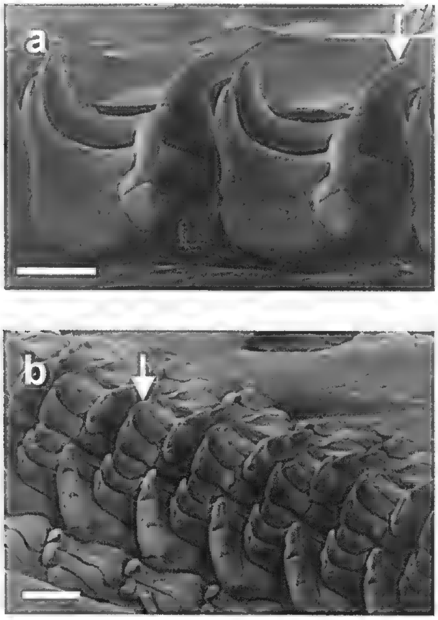

Fig. 1. Scanning electron microscope images of the radula of (*a*) *Patelloida alticostata* (arrow = posterior cusp of the tooth; scale bar = 100 µm) and (*b*) *Scutellastra laticostata* (arrow = an interior major lateral tooth; scale bar = 200 µm).

Patella laticostata), were chosen because they are representative of the extremes of limpet speciation (Lindberg 1998).

Materials and methods

Patelloida alticostata specimens were collected from limestone rocks in the splash zone at low tide in the Perth metropolitan area (32°S, 116°E), whereas *Scutellastra laticostata* specimens were collected from granite rocks at Bunker Bay (34°S, 115°E), also at low tide. Following collection, animals were placed in fresh seawater and transported immediately back to the laboratory, where the radula was dissected out. After removal, the radulae were placed in a solution of 4% NaOCl to remove any contaminating organic material. Once clean, the radulae were then positioned individually between glass slides to keep them flat during subsequent processing and placed directly into 30% ethanol. Radulae were examined at this stage using light microscopy to determine their overall structure, the number of tooth rows and the stage of tooth mineralisation.

The teeth of *P. alticostata* are arranged in a series of double rows with approximately 82 rows of teeth per radula. Each of the major lateral teeth, and there are only two per row, consists of a single anterior and posterior cusp connected by a single tooth base and flanked by a small marginal (Fig. 1*a*). In contrast, the larger *S. laticostata* possesses a much longer radula of approximately 185 tooth rows, the structure of which comprises one central unicuspid tooth flanked by a pair of unicusped inner lateral teeth. These are followed by a tricuspid outer lateral tooth that is set behind the inner row, with an additional three, unicusped marginal teeth set further out again in the radula (Fig. 1*b*). Light microscopy revealed that, in both species, only the lateral teeth were mineralised, as shown by the presence of a brown colouration, and, thus, only these teeth were subjected to analysis. In both species, initial elemental mapping was followed by a series of spot analyses obtained in various regions around the tooth cusp/s, in the junction zone that separates the tooth cusp from the tooth base and in at least three areas in the base.

For scanning electron microscopy, individual radulae were fully dehydrated through a graded series of alcohols. Those destined for morphological examination were dried further, using amyl acetate and critical point drying, mounted onto stubs using carbon tape, coated with carbon and gold, and examined using a Philips XL20 scanning electron microscope (SEM; Philips, Eindhoven, The Netherlands). Radulae destined for energy dispersive spectroscopy (EDS) were taken directly from 100% alcohol and sectioned crudely into lengths suitable for analysis. These sections were then placed flat into rectangular moulds and embedded in an Epon/Araldite mixture. So as to present the teeth in longitudinal section, the blocks were

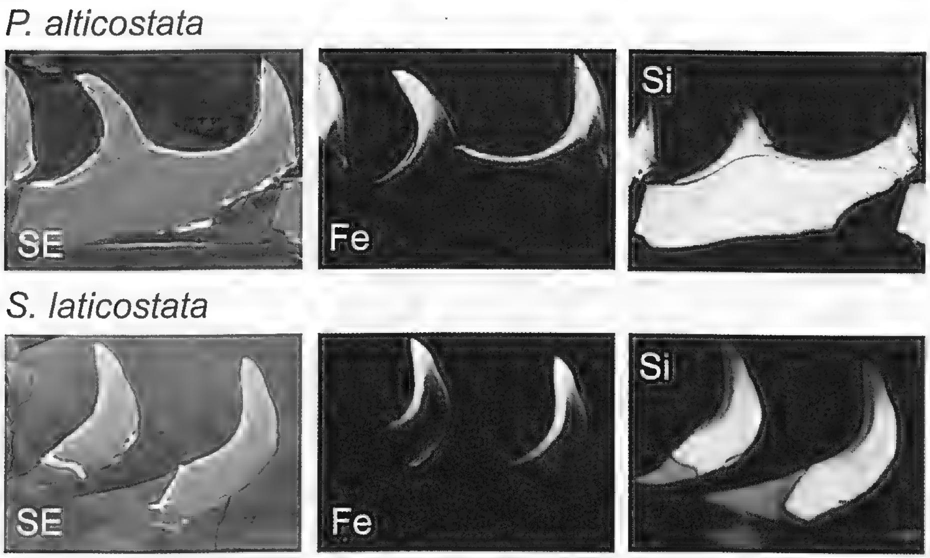

Fig. 2. Typical energy dispersive spectroscopy (EDS) qualitative elemental maps of the major lateral teeth of *Patelloida alticostata* (obtained at tooth row 51) and *Scutellastra laticostata* (obtained at tooth row 84). SE, Secondary electron image; Fe, iron map; Si, silica map.

then re-embedded, in the correct orientation, into aluminium discs. In order to obtain a flat and polished surface for analysis, these discs, together with control discs, were then ground using increasingly fine grades of silicon carbide paper, before being finally polished using a dry macroclean, microfibre cloth to reduce surface relief effects. Discs were cleaned between grades using an ultrasonic cleaner and 3% Extran 300 detergent (EMD Chemicals Inc., Gibbstown, NJ, USA). Discs were then rinsed with two changes of ultrapure water before being evaporative carbon coated. The EDS was performed using an Oxford LINK/ISIS system (Buckingham, UK) with a germanium window and a lithium drifted silicon detector attached to the SEM. Elemental mapping and spot analyses were performed at 20 keV using a spot size of 5 m and a working distance of between 12 and 14 mm. Analyses were performed at regular intervals down the radula of both species, concentrating on regions in which light microscopy indicated rapid changes in mineralisation were occurring. Spot analyses were performed by acquiring at least three spectra from at least eight different regions of the tooth. These regions included the tooth tip, anterior and posterior sides of both anterior and posterior cusps, the junction zone and the tooth base. The EDS system was calibrated every 2 h using a cobalt standard.

Laser Raman spectroscopy was undertaken with an ISA Dilor Labram dispersive spectrometer (Longjumeau cedex, France) using both helium–neon (632.817 nm) and diode (783.532 nm) lasers. Unmineralised teeth were examined at various integration times before embedding, using the diode laser, so that interference due to the resin could be eliminated. Teeth from other stages of development were analysed following the resin embedding described above. Dark current background subtraction was performed on spectra from biological samples, with typical spectra acquisition times ranging from 1 to 6 h. Fourier transform laser Raman spectroscopy was also conducted on siliceous standards with a Bruker RFS-100 spectrometer (Sydney, Australia) using a neodymium:yttrium aluminium garnet (Nd:YAG; 1064 nm) laser and germanium diode detector. Spectra were obtained at 4 cm^{-1} resolution and were equivalent to those obtained with the helium–neon and diode lasers, confirming that these higher-frequency lasers did not degrade the siliceous material. The Raman spectra of the iron oxide and hydroxide standards used have been reported previously (Lee *et al.* 1998). α-Chitin (poly(*N*-acetyl-1,4-β-D-glucopyranosamine)) was obtained as a purified product (Sigma, St Louis, MO, USA), amorphous silica was synthesised using a sol-gel process (Munoz-Aguado and Gregorkiewitz 1997) and α-quartz and naturally occurring opaline silica (in the form of white sedimentary opal) were obtained from the Geology Department at Curtin University.

Infrared microscopy was conducted using a Bruker IFS-66 spectrometer fitted with a nitrogen-cooled EG&G Judson mid-infrared photoconductive mercury cadmium telluride detector system (MIR-MCT;

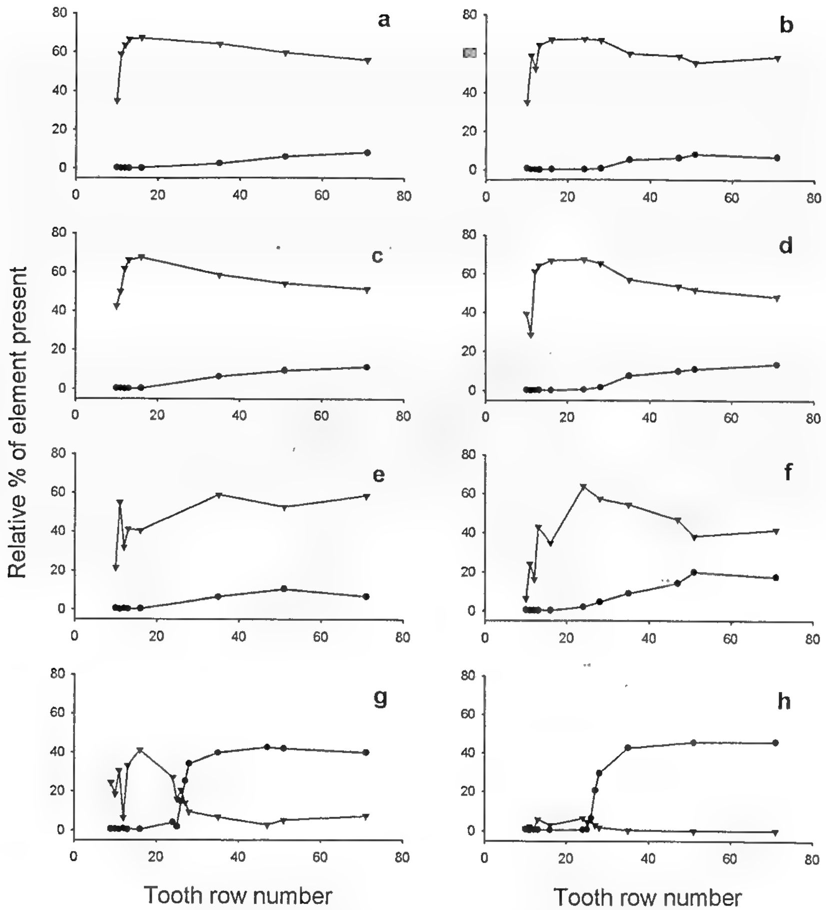

Fig. 3. Mean quantitative elemental spot analysis data of the major lateral teeth of *Patelloida alticostata* at various stages of development down the radula. (*a*) The tip of the anterior cusp; (*b*) the tip of the posterior cusp; (*c*) the posterior region of the anterior cusp; (*d*) the posterior region of the posterior cusp; (*e*) the anterior region of the anterior cusp; (*f*) the anterior region of the posterior cusp; (*g*) the junction zone; and (*h*) the tooth base. ▼, Percentage of iron relative to that of all other elements found; ● percentage of silica.

Montgomeryville, PA, USA) and a Bruker infrared microscope accessory and was collected at 4 cm^{-1} resolution. Synthetic iron oxides, amorphous silica and α-chitin standards were analysed as KBr discs with 512 scans being accumulated, whereas naturally occurring opaline silica and α-quartz standards were analysed by reflection, with an open aperture and 8192 scans being accumulated. Again, unmineralised teeth were analysed by infrared microscopy before the embedding process, so that interference from the resin could be eliminated, using an aperture selectively shaped to contain individual teeth, with 2048 scans being accumulated. Teeth from the later stages of mineralisation were analysed following resin embedding using reflection microscopy, with 8192 scans being accumulated.

Results

In *Patelloida alticostata*, qualitative EDS elemental mapping revealed that mineralisation, as evidenced by an influx of iron, commences in the junction zone at row 9, rapidly spreading to the posterior region of both the anterior and posterior tooth cusps by row 10

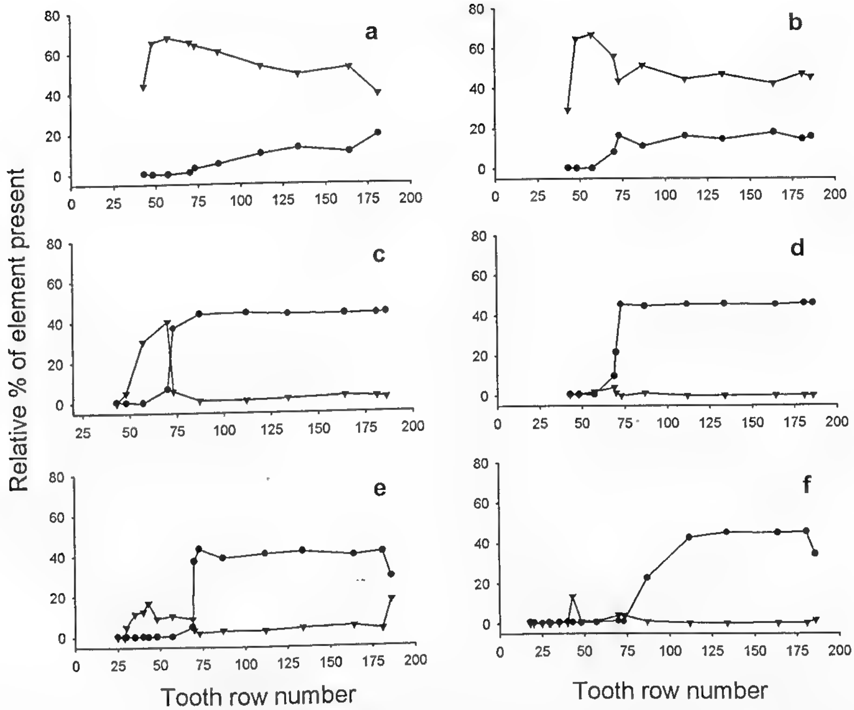

Fig. 4. Mean quantitative elemental spot analysis data of the major lateral teeth of *Scutellastra laticostata* at various stages of development down the radula. (*a*) The cusp tip; (*b*) the posterior region of the cusp; (*c*) the anterior region of the cusp; (*d*) the cusp core; (*e*) the junction zone; and (*f*) the tooth base. ▼, Percentage of iron relative to that of all other elements found; ●, percentage of silica.

and reaching high levels in these two regions by row 15 (an example of the type of map produced is given in Fig. 2). Quantitative multiple spot analysis confirmed the preliminary elemental mapping data, with initial levels of 22% iron being recorded in the junction zone, rising to 40% by row 15 before declining rapidly to less than 10% by row 28 (Fig. 3). In the tip and posterior regions of both the anterior and posterior cusps, iron levels peaked at just under 70% by row 12, declining only gradually down the length of the radula to approximately 60% in the tip and 55% in the posterior surface by the working teeth (Fig. 3). Although iron levels were also high in the anterior region of both the anterior and posterior cusps, the influx of this element occurred relatively slowly in the anterior region of the anterior cusp, not reaching a peak until row 35 (Fig. 3). Much higher iron levels were recorded earlier in the anterior region of the posterior cusp; however, these declined as maturation proceeded.

In contrast with iron, the influx of silica into the teeth of *P. alticostata* both occurred more slowly and was initiated later. Both EDS mapping and spot analyses (Fig. 3) showed that only small amounts of silica (less than 10%) were present in the posterior regions of both the anterior and posterior cusps, even in the fully mature teeth. Slightly more was found in the anterior cusps, but by far the largest amounts were found in the junction zone and the tooth base where silica predominated (Fig. 3). No evidence was found for any other elements, other than those associated with the organic components and the resin, at levels greater than 1%.

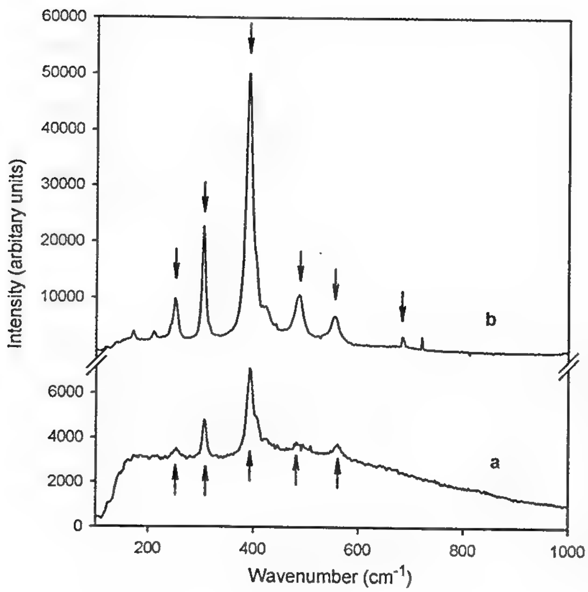

Fig. 5. Raman spectra of (*a*) an early mineralised major lateral tooth of *Patelloida alticostata* indicating the presence of goethite peaks (arrows) on a broad background, and (*b*) a late mineralised tooth of the same species now indicating the presence of strong goethite peaks (arrows) with relatively little background.

In *Scutellastra laticostata*, EDS mapping suggested that mineralisation followed a slightly different pattern (for an example of the type of map produced, see Fig. 2) with data obtained from spot analysis again confirming the initial impressions (Fig. 4). Thus, although the junction zone was again the first region of the tooth to show evidence of the influx of iron, in mature teeth this element was basically confined to the tip and posterior surface of the lateral teeth, with only small amounts being found in other regions of the tooth. The tip and posterior region of the tooth also contained up to 15% silica at the mature end of the radula. In marked contrast with the situation in the cusps of *P. alticostata*, where silica was virtually absent, the remainder of the cusp in *S. laticostata* was occupied almost entirely by silica, with only small amounts of iron being present. However, the composition of the junction zone and base was much more similar to that of *P. alticostata*, again being composed mainly of silica (Fig. 4). Low concentrations of calcium (approximately 3%) were also found early in the mineralisation process in the junction zone, although these declined rapidly (to less than 1%) as mineralisation progressed. Again, no evidence was found for any other elements, other than those associated with the organic components and the resin, at levels greater than 1%.

Raman microscopy of unmineralised teeth from both species revealed only the presence of α-chitin, with no evidence of the presence of iron oxides or siliceous compounds. However, the presence of weak, broad bands of ferrihydrite cannot be discounted. In both species, shortly following the initial deposition of iron, spectra obtained from the posterior surface of the tooth resolved a series of peaks characteristic of goethite (Fig. 5*a*). No evidence was found for the presence of any other minerals in any other regions of the tooth. As mineralisation progressed, the Raman goethite spectra became far more distinct and accounted for almost all the spectral bands observed (Fig. 5*b*). This form of spectroscopy indicated that the occurrence of goethite followed the initial deposition of iron very closely. Thus, for example, by tooth row 51 in *P. alticostata*, spectra positive for the presence of goethite were obtained from throughout the upper section of both the anterior and posterior cusps and in the surface of the 'saddle' region between the two cusps. Similarly, in

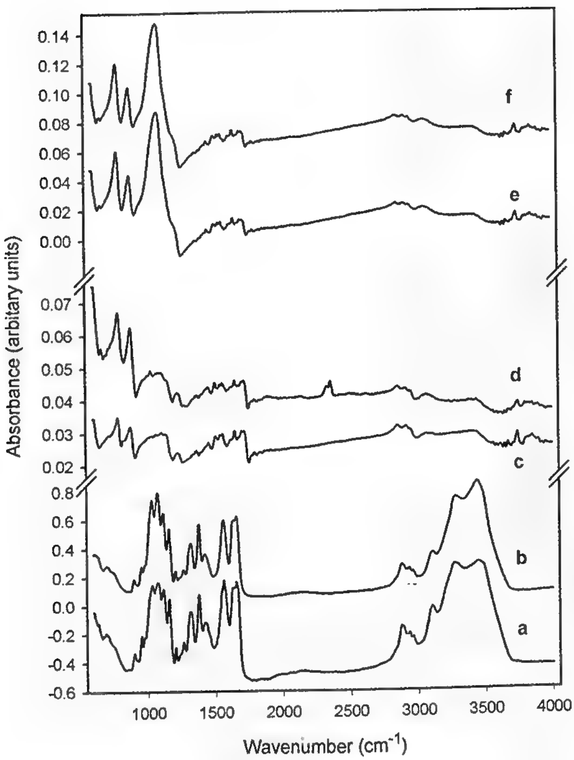

Fig. 6. Infrared spectra of the major lateral teeth of *Patelloida alticostata* (*a*, *c*, *e*) and *Scutellastra laticostata* (*b*, *d*, *f*): before the onset of mineralisation (*a*, *b*); at the onset of mineralisation (*c*, *d*); and later in the mineralisation process (*e*,*f*).

S. laticostata, by row 120, spectra strongly indicative of goethite were obtained from the tip and posterior surface of the cusp, whereas weak goethite spectra were also obtained from the upper anterior region of the cusp.

Infrared spectra of teeth from both species before the onset of mineralisation are presented in Fig. 6*a*,*b*. In both cases, the spectra are in close agreement with that of α-chitin, with the presence of distinct amide peaks in the spectral regions 1552 and 1616–1671 cm^{-1} being particularly useful for diagnostic purposes. There is no evidence of any contribution from ferrihydrite at approximately 1620 cm^{-1} at this stage of development. Early in the mineralisation process, the development of major absorption bands at 500–1000 cm^{-1} can be assigned to the presence of goethite. However, the presence of α-chitin (1250–1700 cm^{-1}) is still very obvious (Fig. 6*c*,*d*). Later in the mineralisation process, infrared spectra from both species were relatively unchanged in the region 500–1100 cm^{-1}, yet an intense peak at 1091 cm^{-1} has appeared that can be assigned to the Si-O-Si stretch of silica (Fig. 6*e*,*f*). The peaks due to α-chitin have also become relatively less intense. Spectra obtained from fully mature teeth (row 140 onwards) are dominated by the 1091 cm^{-1} silica peak, which has become very intense, whereas the peaks at 784 and 875 cm^{-1} have virtually disappeared (data not shown). The absorption bands due to α-chitin (1250–1700 cm^{-1}) have also completely disappeared, with a peak at 775 cm^{-1} becoming evident in both species. This later band can be assigned to the Si-O-Si bending vibration in opaline silica.

Discussion

The data presented in the present study allow, for the first time, a complete picture of the sequence of mineralisation in the major lateral teeth to be constructed in two limpet species,

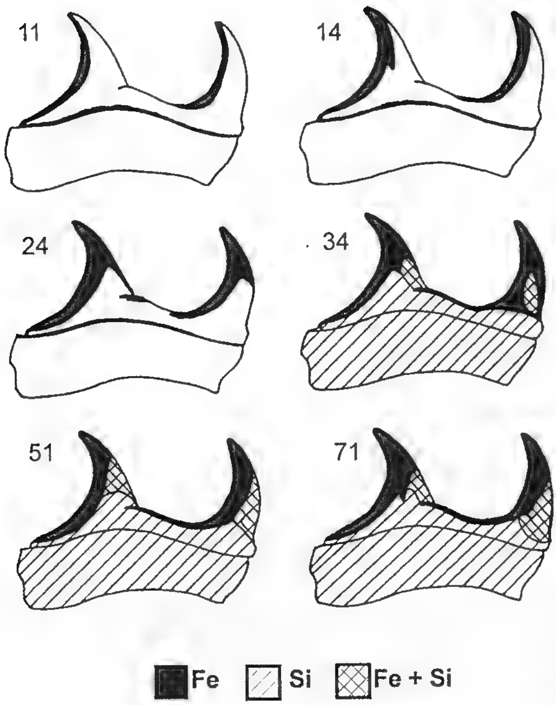

Fig. 7. Schematic representation of elemental inflow and subsequent mineral deposition in *Patelloida alticostata*. Tooth row numbers are indicated above the teeth.

namely *Patelloida alticostata* and *Scutellastra laticostata* (Figs 7, 8). Although specific differences do exist, the general pattern of tooth mineralisation is very similar, suggesting that the mineralisation of iron in particular and, to a lesser extent, silica is a very ancient character in the Patellogastropoda, and possibly in the Mollusca as a group (Cruz *et al.* 1998; Brooker and Macey 2001). However, tooth mineralisation in limpets, with its intermingling of complex mineral forms, is obviously very different from that in chitons, where different minerals are restricted to architecturally discrete compartments (Lowenstam 1967; Lee *et al.* 1998). In both limpet species, the initiation of the mineralisation process, as judged by the initial influx of iron, occurs in the junction zone, the region separating the tooth cusp from the tooth base (Figs 7, 8). In this regard, these two limpet species parallel the mineralisation process in the chitons *Cryptoplax striaita* and *Acanthopleura echinata*, where mineralisation is also initiated in this region (Macey and Brooker 1996; Brooker *et al.* 2003). The presence, in this region, of high levels of iron and, later, silica, seen using EDS, without the subsequent large-scale deposition of minerals in the same area, also suggests that the junction zone acts as an initial reservoir, or conveyor, of material, allowing these elements to build up to a critical concentration before the onset of mineralisation proper in the upper regions of the posterior surface of the teeth and, thus, plays a very active role in the process (Macey and Brooker 1996; Brooker *et al.* 2003). Although these results would appear to be in contrast with those of previous authors who have suggested that mineralisation in limpets occurs initially in the tooth base, followed by the posterior surface of the tooth cusp (see, for example, Grime *et al.* 1985; Mann *et al.* 1986; Rinkevich 1993), the range of techniques used in the present study allows a far more detailed picture of both elemental and mineral deposition to be established. Although these

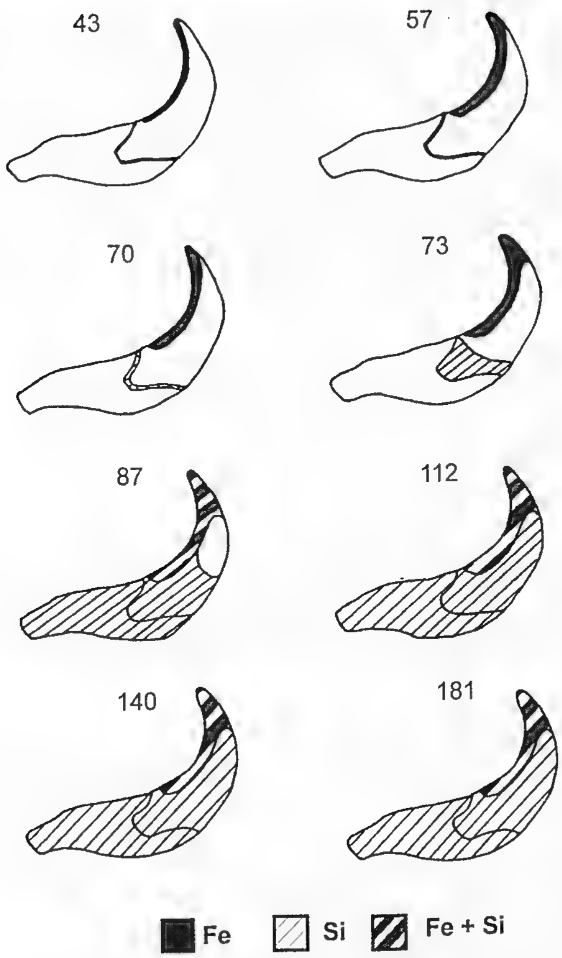

Fig. 8. Schematic representation of elemental inflow and subsequent mineral deposition in *Scutellastra laticostata*. Tooth row numbers are indicated above the teeth.

differences could be attributed to species variation, the deliberate choice in the present study of very divergent limpet species (Lindberg 1998), together with the parallel occurrence of the same phenomenon in chitons (Macey and Brooker 1996; Brooker *et al.* 2003), suggests that the initiation of the mineralisation process, where it occurs, through the junction zone is possibly widespread in molluscan teeth.

The very rapid spread of iron in the posterior surface of the tooth cusps of both species, following on from its initial appearance in the junction zone, may well be related to the need to allow for subsequent slow crystal growth in a favoured direction. Indeed, the presence of stoichiometric, well-ordered crystals in this region, in contrast with the superparamagnetic, poorly ordered microcrystals located within the tooth base, has been noted previously (Mann *et al.* 1986; St Pierre *et al.* 1986). In contrast, in both species both the deposition and mineralisation of silica occur much later in tooth development, possibly reflecting the less-ordered structure of the 'scrolls' formed (Mann *et al.* 1986). The presence in the tooth bases of large amounts of silica, presumably in the form of loosely aggregated scrolls, rather than crystalline goethite may well be due to the need for the base to be more flexible than the cusp, allowing for the impact of the tooth cusp striking the hard surfaces on which the limpets feed.

The relationship between tooth structure, in terms of the number of overall impact points and the degree of mineralisation has been well established across a wide variety of molluscan species (Steneck and Watling 1982). The reduced number of impact points in *P. alticostata* (four), compared with the far larger number in *S. laticostata* (10), is paralleled both by a far greater proportion of the tooth cusp being mineralised with iron in the former species and by the complete lack of silica in the posterior cusp surface of *P. alticostata*. All these factors suggest that the cutting surface of the major lateral teeth in *P. alticosata* is much harder that that of *S. laticostata*, indicating, in turn, that the two species have very different feeding habits, with *P. alticostata* penetrating into the substratum on which it is found to much greater degree than *S. laticostata* (Black *et al.* 1988).

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References

Black, R., Lymbery, A., and Hill, A. (1988). Form and function: size of radular teeth and inorganic content of faeces in a guild of grazing molluscs at Rottnest Island, Western Australia. *Journal of Experimental Marine Biology and Ecology* **121**, 23–35. doi:10.1016/0022-0981(88)90021-4

Brooker, L. R., and Macey, D. J. (2001). Biomineralization in chiton teeth and its usefulness as a taxonomic character in the genus *Acanthopleura* Guilding, 1929 (Mollusca: Polyplacophora). *American Malacological Bulletin* **16**, 203–215.

Brooker, L. R., Lee, A. P., Macey, D. J., van Bronswijk, W., and Webb, J. (2003). Multiple-front iron mineralisation in chiton teeth (Mollusca: Polyplacophora). *Marine Biology* **142**, 447–454.

Burford, M. A., Macey, D. J., and Webb, J. (1986). Hemolymph ferritin and radula structure in the limpets *Patelloida alticostata* and *Patella peronii* (Mollusca: Gastropoda). *Comparative Biochemistry and Physiology* **83A**, 353–358.

Cruz, R., Lins, U., and Farina, M. (1998). Minerals of the radular apparatus of *Falcidens* sp. (Caudofoveata) and the evolutionary implications for the phylum Mollusca. *The Biological Bulletin* **194**, 224–230.

Grime, G. W., Watt, F., Mann, S., Perry, C. C., Webb, J., and Williams, R. J. P. (1985). Biological applications of the Oxford scanning microprobe. *Trends in Biochemical Sciences* **10**, 6–10.

Jones, E. I., McCance, R. A., and Shackleton, L. R. B. (1935). The role of iron and silica in the structure of the radular teeth of certain marine molluscs. *Journal of Experimental Biology* **12**, 59–64.

Kim, K.-S., Macey, D. J., Webb, J., and Mann, S. (1989). Iron mineralization in the radula teeth of the chiton *Acanthopleura hirtosa*. *Proceedings of the Royal Society Series B* **B237**, 335–346.

Lee, A. P., Webb, J., Macey, D. J., van Bronswijk, W., Savarese, A., and De Witt, C. (1998). *In situ* Raman spectroscopic studies of the teeth of the chiton *Acanthopleura hirtosa*. *Journal of Biological Inorganic Chemistry* **3**, 614–619. doi:10.1007/S007750050274

Lindberg, D. R. (1998). Order Patellogastropoda. In 'Mollusca: The Southern Synthesis. Fauna of Australia'. (Eds P. L. Beesley, G. J. B. Ross and A. Wells.) pp. 565–1234. (CSIRO Publishing: Melbourne, Australia.)

Lowenstam, H. A. (1962*a*). Magnetite in denticle capping in recent chitons (Polyplacophora). *Bulletin of the Geological Society of America* **73**, 435–438.

Lowenstam, H. A. (1962*b*). Goethite in radular teeth of recent marine gastropods. *Science* **137**, 279–280.

Lowenstam, H. A. (1967). Lepidocrocite, an apatite mineral, and iron teeth of chitons (Polyplacophora). *Science* **156**, 1373–1375.

Lowenstam, H. A., and Weiner, S. (1989). 'On Biomineralization.' (Oxford University Press: Oxford, UK.)

Lu, H.-K., Huang, C.-M., and Li, C.-W. (1995). Translocation of ferritin and biomineralization of goethite in the radula of the limpet *Cellana toreuma* Reeve. *Experimental Cell Research* **219**, 137–145. doi:10.1006/EXCR.1995.1214

Macey, D. J., and Brooker, L. R. (1996). The junction zone: the initial site of mineralization in the radula teeth of the chiton *Cryptoplax striata* (Mollusca: Polyplacophora). *Journal of Morphology* **230**, 33–42. doi:10.1002/(SICI)1097-4687(199610)230:1<33::AID-JMOR3>3.0.CO;2-O

Mann, S., Perry, C. C., Webb, J., Luke, B., and Williams, R. J. P. (1986). Structure, morphology, composition and organization of biogenic minerals in limpet teeth. *Proceedings of the Royal Society Series B* **B227**, 179–190.

Munoz-Aguado, M.-J., and Gregorkiewitz, M. (1997). Sol-gel synthesis of micorporous amorphous silica from purely inorganic precursors. *Journal of Colloid and Interface Science* **185**, 459–465. doi:10.1006/JCIS.1996.4564

Rinkevich, B. (1993). Major primary stages of biomineralization in radula teeth of the limpet *Lottia gigantea. Marine Biology* **117**, 269–277.

Runham, N. W., and Thornton, P. R. (1967). Mechanical wear of the gastropod radula: a scanning electron microscope study. *Journal of Zoology* **153**, 445–452.

Runham, N. W., Thornton, P. R., Shaw, D. A., and Wayte, R. C. (1969). The mineralization and hardness of the radular teeth of the limpet *Patella vulgata. Zeitschrift fur Zellforschung und Mikroskopische Anatomie* **99**, 608–626.

St Pierre, T. G., Mann, S., Webb, J., Dickson, D. P. E., Runham, N. W., and Williams, R. J. P. (1986). Iron oxide biomineralization in the radula teeth of the limpet *Patella vulgata*: Mossbauer spectroscopy and high resolution transmission electron microscopy. *Proceedings of the Royal Society Series B* **B228**, 31–42.

Steneck, R. S., and Watling, L. (1982). Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Marine Biology* **68**, 299–319.

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Growth, reproduction and recruitment of the endangered brackish water snail *Iravadia* (*Fairbankia*) *sakaguchii* (Gastropoda : Iravadiidae)

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Abstract

The population structure and reproductive activity of the brackish water snail *Iravadia* (*Fairbankia*) *sakaguchii*, which lives under partially buried stones on intertidal mudflats, were investigated monthly in the Waka River Estuary, Wakayama, central Japan. Observations of the reproductive organs indicated the main reproductive season as being from June to July. Maturation size was estimated to be approximately 4.0 mm in shell length (SL) in females and 3.9 mm SL in males, there being no significant sexual dimorphism in adult body size. The occurrence of snails smaller than 2 mm SL indicated that recruitment occurred between August and October, all the recruits co-occurring with adults under stones. The recruits grew to a large size (>3 mm SL) and reached maturity in August of the second year (1 year old), longevity being estimated as at least 37–38 months. Throughout the study period of 28 months, the population mostly comprised individuals between 3 and 5 mm SL, with recruits being fewer than older snails. The population density decreased each year, this being attributable to a low level of recruitment.

Additional keywords: tidal flat.

Introduction

Iravadia (*Fairbankia*) *sakaguchii* (Kuroda & Habe, 1954) is a small (usually less than 6 mm in shell length (SL)) gastropod belonging to the family Iravadiidae (superfamily Rissooidea). The family occurs worldwide, although most species are found in the Indo-West Pacific region, their habitat usually being in estuaries or enclosed bays (Ponder 1984). Although some taxonomic studies of the family have been conducted (e.g. Ponder 1984, 1994; Beu and Maxwell 1990; Dockery 1993), there appear to have been no ecological studies on life history or population dynamics.

Iravadia sakaguchii is endemic to Japan and has been recorded at several locations, including Wakaura Bay, Wakayama (type locality), Ariake Sound, Sea of Suou, the Seto Inland Sea, Ise Bay and Mikawa Bay (Kimura 1987, 1989; Fukuda *et al.* 1990; Murohara 2000; Kimura *et al.* 2001). Because of its limited distribution, the species has been assessed as 'endangered' (Wada *et al.* 1996). Nevertheless, there have been only fragmentary studies on habitat conditions undertaken to date (Fukuda *et al.* 1990; Kimura and Kimura 1999; Kobayashi *et al.* 2003).

Iravadia sakaguchii is known to live under partially buried stones or hard materials on mudflats in brackish water (Fukuda *et al.* 1990; Hosaka and Fukuda 1996; Kobayashi *et al.* 2003). Ecological studies of benthos in this type of habitat have not received much attention because of the inherent difficulties in field observations. The aim of the present study was to reveal the life history and provide an understanding of the population ecology of *I. sakaguchii*.

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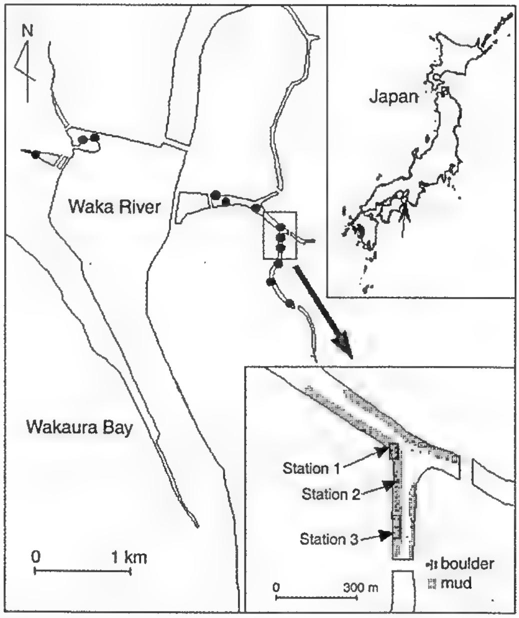

Fig. 1. Map showing locations of the study sites (stations 1–3) in the Waka River Estuary, central Japan. Solid circles indicate where *Iravadia sakaguchii* occurred.

Materials and methods

Seasonal changes in population structure

The present study was conducted on an intertidal mudflat in the Waka River Estuary, Wakayama, central Japan (34°10′N, 135°10′E; Fig. 1). Three stations (stations 1, 2 and 3) where *I. sakaguchii* occurred were selected along a tributary of the Waka River, with intertidal heights varying from –29 to 14 cm above mean sea level. Stations 1 and 3 were areas of stones on mud (station 1: 1.5×2 m^2 (number of stones: 32); station 3: 1.6×8 m^2 (number of stones: 181)), whereas station 2 consisted of an artificial block ($55 \times 44 \times 4.5$ cm in height) on mud. Water salinity near the stations, recorded over 24 h on 3 and 4 July 2000, varied from 1.6 to 29.4. The silt-clay content of the mud, recorded by grain size analysis according to the Wentworth classification, ranged from 16.3% to 73.4% ($n = 15$; Kobayashi *et al.* 2003).

Populations of *I. sakaguchii* at the three stations were monitored during periods of daytime low tide every 2 months from March 2000 to April 2001 and once a season (August, October, January, April and August) from August 2001 to August 2002. At each station, all stones were overturned and snails found underneath the stones or on the mud were picked up with tweezers. Each of the snails collected was set on a Petri dish (90 mm in diameter), aperture facing upwards, with 1-mm graph paper to measure the SL (from the apex to the anterior margin of the aperture) to the nearest 0.5 mm. After being measured, the snails were replaced carefully in their original positions under the stones.

Reproductive activities

To investigate the reproductive stages of the snails, 19–24 snails larger than 3 mm SL were collected near station 1 monthly from December 2001 to November 2002. These specimens were preserved in the laboratory at –5°C. The SL of each snail was measured (from the apex to the anterior margin of the aperture) to the nearest 0.1 mm with a vernier micrometre. Measured specimens were then soaked in 70% hydrochloric acid solution for approximately 30 min to dissolve the shell. Specimens were then dissected under a binocular microscope, sex being determined according to the presence of female or male reproductive organs. Snails were classified into five groups according to reproductive stage, which was determined by the relative sizes of the reproductive organs (female: albumen gland, capsule gland and bursa copulatrix; male: prostate, penis and testis) as shown in Tables 1 and 2.

Table 1. Reproductive stages classified according to the relative size of reproductive organs and gonad conditions in female *Iravadia sakaguchii*

Ag+Cg	Bursa copulatrix	Ovary	Stage
iv	iv	iv	f1
s	iv	iv	f2
s	iv	v	f3
l	iv	v	f4
l	v	v	f5

Ag, Albumen gland; Cg, capsule gland; iv, invisible; v, visible; s, small; l, large.

Table 2. Reproductive stages classified according to the relative size of reproductive organs and gonad condition in male *Iravadia sakaguchii*

Penis	Prostate	Testis	Stage
s	iv	iv	m1
m	iv	iv	m2
m	s	v	m3
l	s	v	m4
l	l	v	m5

iv, Invisible; v, visible; s, small; m, middle; l, large.

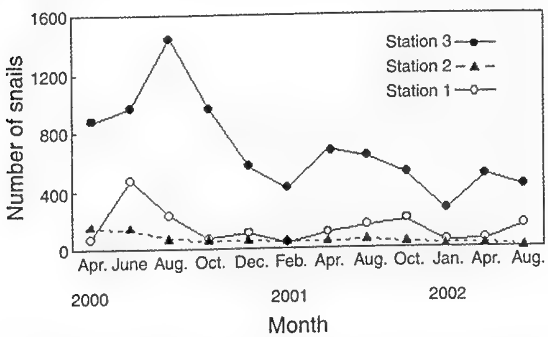

Fig. 2. Monthly changes in snail numbers at stations 1–3 from April 2000 to August 2002.

Results

Seasonal and yearly changes in population density

Numbers of *I. sakaguchii* showed seasonal fluctuations during the study period at stations 1 and 3, increasing between spring and summer and declining between autumn and winter (Fig. 2). However, at station 2, the number of snails did not exhibit any particular seasonal fluctuation.

The maximum number of snails was recorded in spring–summer in each of the study years at stations 1 and 3 (Fig. 2). The peak number of snails decreased each year, being highest in 2000 and lowest in 2002 with only half the number of snails found in 2002 compared with 2000. At station 2, the number of snails decreased continuously throughout the study period, dropping to only three snails by August 2002.

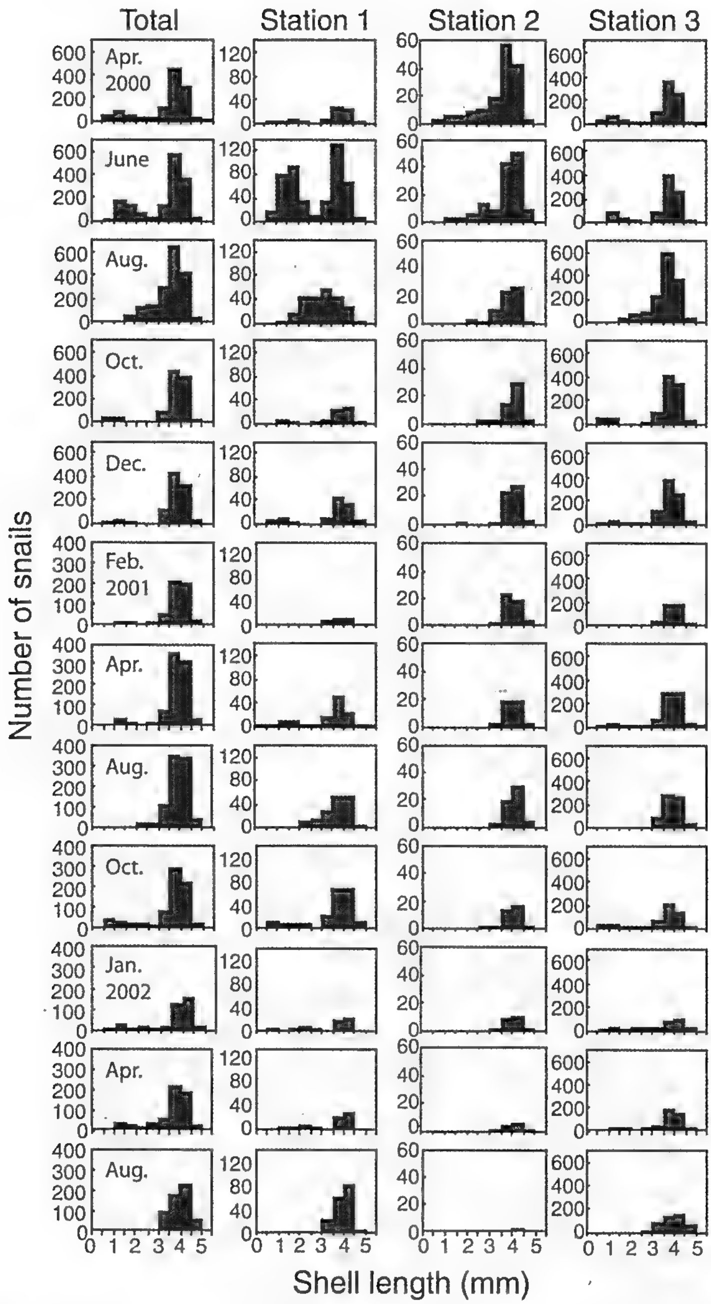

Fig. 3. Frequency distributions of shell lengths of *I. sakaguchii* at stations 1–3 from April 2000 to August 2002.

Seasonal changes in size structure

The populations at the three stations consisted mostly of individuals of 3–5 mm SL during the study period (Fig. 3). The occurrence of snails smaller than 2 mm SL at stations 1 and

3 between August and October in both 2000 and 2001 indicated that recruitment occurred during these periods. Successive changes in length–frequency histograms (Fig. 3) showed that recruits scarcely grew until the following April, but then grew to a large size by the following August (1 year old). After the snails were 1 year old, growth could not be determined from histograms.

Survivorship is estimated from station 2 data as follows. Because station 2 was isolated by approximately 50 m from other populations owing to a lack of suitable habitat, migration of snails into the station was unlikely, considering the data on individual movement obtained by Kobayashi *et al.* (2003), in which the maximum movement observed for 228 marked snails during 4 months was 1.6 m at most. Furthermore, recruitment scarcely occurred at station 2 in 2000 and 2001 (Fig. 3), with large-sized snails found at the end of the study period (August 2002) appearing to have survived throughout the study period (28 months). If this was the case, the large-sized snails in April 2000 at station 2 can be regarded as having been recruited in 1999 and must be at least 9–10 months old. Consequently, longevity can be estimated as at least 37–38 months (=3.1–3.2 years).

The number of small-sized individuals (<3 mm SL, <1 year old) varied among stations as well as among years (Fig. 3). At station 3, small-sized snails were recorded in all three years (1999, 2000 and 2001), although their abundance was low relative to that of large-sized snails (3–5 mm SL). At station 2, no small-sized snails were observed after February 2001. At station 1, smaller snails were collected in all three years, but their abundance in June 2000 was greater than in other periods, indicating that recruitment at station 1 in 1999 was greater than in the other years and greater than that at stations 2 and 3 over the 3-year period.

Distribution of recruits

The small-sized snails appearing in October (recruits) were found under 17 of 181 stones (9.4%) in 2000 and under 15 of 181 stones (8.3%) in 2001. Those stones were inhabited by both recruits and adults (larger than 4 mm SL). The number of recruits and adults under the same stone were significantly positively correlated in 2001 ($r^2 = 0.69$, $P < 0.05$, $n = 15$), whereas no significant correlation was found in 2000 ($r^2 = 0.02$, $P > 0.05$, $n = 17$).

Reproductive activities

All snails dissected had either female or male organs and the sex ratio was significantly female biased (92 males *v.* 162 females; Binomial test: $P < 0.05$). The size frequency distribution of each sex in snails larger than 3 mm SL indicated that no significant difference in size existed between males and females throughout the year (Mann–Whitney *U*-test: $P > 0.05$; Fig. 4).

Developmental conditions of the reproductive organs showed seasonal changes in both males and females (Fig. 5), the range of body sizes at different reproductive stages overlapping widely (Table 3). From the smallest snail sizes at stage 5, maturation was determined as having been attained at 4.0 mm SL in females and 3.9 mm SL in males.

Female snails at stage 5 occurred in January and February and April–October, with a peak in July. Male snails at stage 5 occurred in May–December, with a peak in June.

Discussion

Monthly changes in the development of the reproductive organs in *I. sakaguchii* showed that the most developed stage occurred most frequently in June (males) and July (females), indicating that those summer months were the main reproductive season. The reproductive

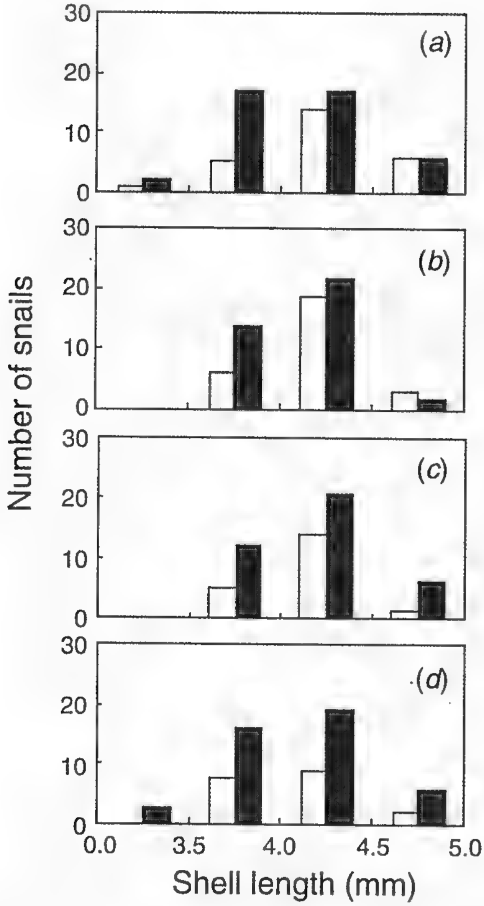

Fig. 4. Seasonal changes in frequency distributions of shell lengths of *I. sakaguchii* females (solid) and males (open). (*a*) December to February; (*b*) March to May; (*c*) June to August; (*d*) September to November.

season of other temperate region species of rissooideans (approximately 5–15 mm SL) living in brackish water varies considerably as follows: spring for *Assiminea japonica* Martens, 1877 (Kurata and Kikuchi 2000), summer for *Hydrobia ventrosa* (Montagu, 1803) (Barnes 1990) and *Angustassiminea castanea* (Westerlund, 1883) (Kurata and Kikuchi 2000), and late winter–spring and summer–autumn for *Hydrobia ulvae* (Pennant, 1777) (Anderson 1971; Fish and Fish 1974; Bachelet and Yacine-Kassab 1987; Barnes 1990; Haubois *et al.* 2002).

Simultaneous hermaphroditism and protandry are known in some gastropods (Sumikawa 1994), but there is no indication of this in *I. sakaguchii*.

The occurrence of snails smaller than 2 mm SL indicated that recruitment occurred from August to October (Fig. 3). The abundance of recruits recorded in October was much lower than that of older snails at all stations in both 2000 and 2001, suggesting a low level of recruitment in both years. There were fewer small-sized snails in June 2000 than large-sized snails, indicating a low level of recruitment relative to adult abundance in 1999. This low

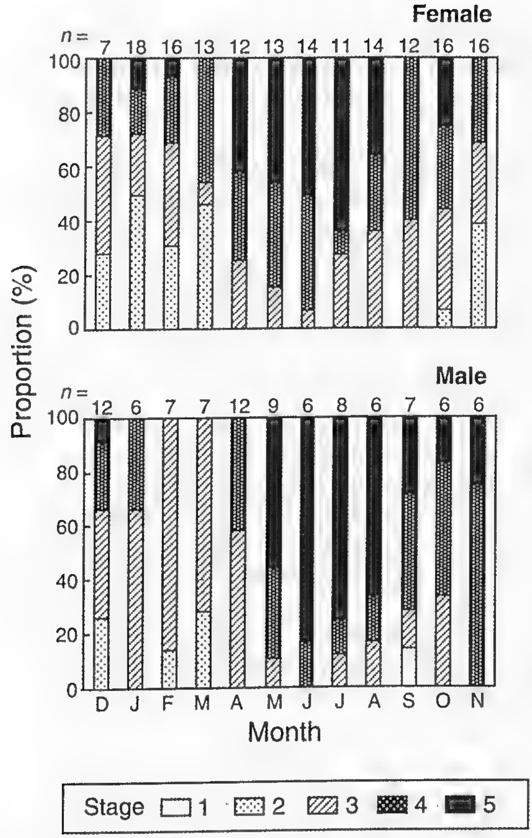

Fig. 5. Monthly changes in reproductive stages of females and males from December 2001 to November 2002. Reproductive stages (1–5) classified according to reproductive organ condition.

Table 3. Range of shell lengths for each reproductive stage in male and female *Iravadia sakaguchii*

Stage	Shell length (mm)	
	Male	Female
1	3.0	–
2	3.8–4.0	3.5–4.4
3	3.5–4.4	3.2–4.8
4	3.5–4.8	3.6–4.9
5	3.9–4.5	4.0–4.7

level of recruitment may be caused by low levels of reproductive activity and/or high mortality of larvae and juveniles. Life history studies of other rissooid species have shown that the abundance of recruits is generally higher than that of large-sized snails, although the number of recruits fluctuated with time and place (e.g. *H. ulvae* (Chatfield 1972; Anderson 1971; Fish and Fish 1974; Bachelet and Yacine-Kassab 1987; Barnes 1990; Drake and Arias 1995; Sola 1996; Cardoso *et al.* 2002), *H. ventrosa* (Siegismund 1982;

Drake and Arias 1995), *Hydrobia neglecta* Muss, 1963 (Siegismund 1982; Drake and Arias 1995), *A. japonica* (Kurata and Kikuchi 1999; Tashiro *et al.* 2001) and *Assiminea grayana* Fleming, 1828 (Fortuin *et al.* 1981)). In the case of *A. castanea*, recruits were much less abundant than large-sized snails over a 2-year period (Kurata and Kikuchi 1999), as observed for *I. sakaguchii.*

Recruitment occurred at stations 1 and 3 in both 2000 and 2001, but did not occur at station 2 in either year. No recruitment at station 2 may be due to the artificial substrate at this station, but comparisons of recruitment between artificial and natural substrate at the same location are needed to clarify this.

The co-occurrence of adults and recruits in the same living space and the positive relationship between adults and recruit abundance suggest that recruitment may be related to the presence of adults. *Iravadia sakaguchii* is assumed to have a pelagic larval veliger stage based on the figure of the protoconch in Fukuda *et al.* (1990, fig. 2). If this is the case, our data suggest that veligers may settle preferentially in an adult habitat.

Snails grow to a large size (>3 mm SL) by August of the second year (1 year old). Because the shell length at maturity is approximately the same in both sexes (4 mm in females, 3.9 mm in males), it is likely that snails reach maturity during their second summer. Barnes (1990) reported that *H. ulvae* matured after approximately 0.8 of a year of benthic life. However, other estimates gave maturation in this species at almost 2 years (Anderson 1971) or at approximately 1 year (Chatfield 1972; Fish and Fish 1974). Kurata and Kikuchi (2000) estimated that *A. japonica* matured at 1.4 years and that *A. castanea* matured at 0.8 of a year. Thus, the age at maturity of *I. sakauchii* is somewhat similar to those of other rissooid species.

The longevity of *I. sakaguchii* was estimated to be approximately 3.1–3.2 years, whereas that of *H. ulvae* has been estimated as approximately 2.0–2.5 years (Fish and Fish 1974) or approximately 1–2 years (Sola 1996; Cardoso *et al.* 2002). Longevity has been estimated as approximately 1.0–1.5 years in *H. ventrosa* and *H. neglecta* (Drake and Arias 1995), 2.6–3.0 years in *A. japonica* and 4.6 years in *A. castanea* (Kurata and Kikuchi 1999) and 1.5–2.0 years in *Assiminea grayana* (Fortuin et al. 1981). Therefore, *I. sakaguchii* may have greater longevity than most other species of Hydrobiidae and Assimineidae.

The number of *I. sakaguchii* individuals found at the sampling sites increased in warm seasons and decreased in cold seasons. The increase in the number of snails from winter to spring may be due to recruitment during this period or differences in sampling success between winter and spring. However, data on size structure make the former possibility unlikely, whereas observations on activity patterns in the laboratory, which showed that the proportion of active snails, whether floating or crawling, was higher in summer than in winter (Kobayashi *et al.* 2003), support the latter. Low activity in cold seasons would lead to a low discovery rate.

The number of snails in warm seasons decreased in subsequent years during the study period, this being attributable to low levels of recruitment in 2000 and 2001. If *I. sakaguchii* is characterised by low levels of recruitment, low mortality or extended longevity is required to maintain the population. In fact, the species has greater longevity than most other related species, although mortality rates were not examined in the present study. Nevertheless, the population density decreased during the duration of the study. Thus, sporadic successful recruitment, which is known in other long-lived benthos (Bouman and Lewis 1977; Peason and Munro 1991; Nakaoka 1993), is required to maintain this species population. However, another possible reason for the decrease in population density is mortality caused by repeated sampling disturbance and this requires further testing in future studies.

Our observations on the life history traits of *I. sakaguchii* have some relevance to the conservation of this endangered species. A low level of recruitment, positive co-occurrence of recruits and adults and greater longevity suggest that the long-term conservation of adults is critically important for maintaining populations. Consequently, even temporal modification or removal of adult habitat, which is often sparse and widely separated, will probably lead to the rapid decline or local extinction of populations. Thus, protection of the adult habitat against human disturbance is required to assure the long-term survival of this species.

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References

Anderson, A. (1971). Intertidal activity, breeding and the floating habit of *Hydrobia ulvae* in the Ythan Estuary. *Journal of the Marine Biological Association of the UK* **51**, 423–437.

Bachelet, G., and Yacine-Kassab, M. (1987). Integration de la phase post-recrutee dans la dynamique des populations du gasteropode intertidal *Hydrobia ulvae* (Pennant). *Journal of Experimental Marine Biology and Ecology* **111**, 37–60. doi:10.1016/0022-0981(87)90019-0

Barnes, R. S. K. (1990). Reproductive strategies in contrasting populations of the coastal gastropod *Hydrobia ulvae*. Longevity and life-time egg production. *Journal of Experimental Marine Biology and Ecology* **138**, 183–200. doi:10.1016/0022-0981(90)90166-A

Beu, A. G., and Maxwell, P. A. (1990). Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **58**, 1–518.

Bouman, R. S., and Lewis, J. R. (1977). Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the UK* **57**, 793–815.

Cardoso, G., Lillebo, A. I., Pardal, M. A., Ferreira, S. M., and Marques, J. C. (2002). The effect of different primary producers on *Hydrobia ulvae* population dynamics: a case study in a temperate intertidal estuary. *Journal of Experimental Marine Biology and Ecology* **277**, 173–195. doi:10.1016/S0022-0981(02)00338-6

Chatfield, J. E. (1972). Study on variation and life history in the prosobranch *Hydrobia ulvae* (Pennant). *Journal of Conchology* **27**, 463–473.

Dockery, D. T. (1993). The streptoneuran gastropods, exclusive of the Stenoglossa, of the Coffee Sand (Campanian) of northeastern Mississippi. *Missisppi Department of Environmental Quality, Office of Geology, Bulletin* **129**, 1–191.

Drake, P., and Arias, A. M. (1995). Distribution and reproduction of three *Hydrobia* species (Gastropoda: Hydrobiidae) in a shallow coastal lagoon in the Bay of Cadiz, Spain. *The Journal of Molluscan Studies* **61**, 185–196.

Fish, J. D., and Fish, S. (1974). The breeding cycle and growth of *Hydrobia ulvae* in the Dovey Estuary. *Journal of the Marine Biological Association of the UK* **54**, 685–697.

Fortuin, A. W., Wolf, D. L., and Catharina, H. B. (1981). The population structure of *Assiminea grayana* Fleming, 1828 (Gastropoda, Assimineidae), in the South-West Netherlands. *Basteria* **45**, 73–78.

Fukuda, H., Maeda, K., and Kawabe, K. (1990). The occurrence of *Iravadia* (*Fairbankia*) *sakaguchii* (Kuroda & Habe) in the Inland Sea of Japan, and a note on the nomenclature. *Nankiseibutu* **32**, 103–108. [In Japanese.]

Haubois, A.-G., Guarini, J.-M., Richard, P., Blanchard, G. F., and Sauriau, P.-G. (2002). Spatio-temporal differentiation in the population struture of *Hydrobia ulvae* on an intertidal mudflat (Marennes-Oleron Bay, France). *Journal of the Marine Biological Association of the UK* **82**, 605–614. doi:10.1017/S0025315402005945

Hosaka, K., and Fukuda, H. (1996). Discovery of a population of an endangered brackish-water snail *Stenothyra japonica* (Gastropoda: Neotaenioglossa: Stenothyridae) and characteristics of the accompanied molluscan fauna in Onoda City, Yamaguchi Prefecture, western Japan, with a comment on the conservation value. *The Yuriyagai: Journal of the Malacozoological Association of Yamaguchi* **4**, 65–69.

Kimura, S. (1987). Record of *Iravadia (Faibankia) sakaguchii* from Ariake Sound. *Nankiseibutu* **29**, 95. [In Japanese.]

Kimura, S. (1989). Record of *Iravadia (Faibankia) sakaguchii* from Shiokawa Lagoon (Mikawa Bay). *Nankiseibutu* **31**, 130–131. [In Japanese.]

Kimura, S., and Kimura, T. (1999). The gastropod fauna of the marshes of the reed (*Phragmites australis* (Cav.)) in the estuaries in Mikawa Bay and Ise Bay, Japan. *Japanese Journal of Benthology* **54**, 44–56. [In Japanese.]

Kimura, S., Nomoto, A., Nakanishi, Y., and Sugino, N. (2001). Rediscovery of *Iravadia* (*Fairbankia*) *sakaguchii* (Gastropoda, Sorbeoconcha, Iravadiidae) in Wakaura, Wakayama City, middle Japan. *Nankiseibutu* **43**, 38–40. [In Japanese.]

Kobayashi, Y., Wada, K., and Sugino, N. (2003). Factors affecting the distribution of a brackish water snail, *Iravadia* (*Fairbankia*) *sakaguchii* (Gastropoda:Iravadiidae). *Japanese Journal of Benthology* **58**, 3–10. [In Japanese.]

Kurata, K., and Kikuchi, E. (1999). Life cycle and production of *Assiminea japonica* V. Martens and *Angustassiminea castanea* (Westerlund) at a reed marsh in Gamo Lagoon, northern Japan (Gastropoda: Assimineidae). *Ophelia* **50**, 191–214.

Kurata, K., and Kikuchi, E. (2000). Comparisons of life-history traits and sexual dimorphism between *Assiminea japonica* and *Angustassiminea castanea* (Gastropoda: Assimineidae). *The Journal of Molluscan Studies* **66**, 177–196. doi:10.1093/MOLLUS/66.2.177

Kuroda, T., and Habe, T. (1954). New aquatic gastropods from Japan. *Venus (Journal of the Malacological Society of Japan)* **18**, 71–79.

Murohara, S. (2000). Record of *Iravadia* (*Fairbankia*) *sakaguchii* from Oita Prefecture and Hukuoka Prefecture (Suou Nada Sea). *Kyushunokai* **55**, 39–42. [In Japanese.]

Nakaoka, M. (1993). Yearly variation in recruitment and its effect on population dynamics in *Yoldia notabilis* (Mollusca: Bivalvia), analyzed using projection matrix model. *Research on Population Ecology* **35**, 199–213.

Peason, R. G., and Munro, J. L. (1991). Growth, mortality and recruitment rates of giant clams, *Tridacna gigas* and *T. derasa*, at Michaelmas Reef, central Great Barrier Reef, Australia. *Australian Journal of Marine and Freshwater Research* **42**, 241–262.

Ponder, W. F. (1984). A review of the genera of the Iravadiidae (Gastropoda: Rissoacea) with an assessment of the relationships of the family. *Malacologia* **25**, 21–71.

Ponder, W. F. (1994). The anatomy and relationships of three species of vitrinelliform gastropods from Hong Kong (Caenogastropoda: Rissooidea). In 'The Malacofauna of Hong Kong and Southern China 3: Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China', 13 April–1 May 1992, Hong Kong. (Ed. B. Morton.) pp. 243–281. (Hong Kong University Press: Hong Kong.)

Siegismund, H. R. (1982). Life cycle and production of *Hydrobia ventrosa* and *H. neglecta* (Mollusca: Prosobranchia). *Marine Ecology Progress Series* **7**, 75–82.

Sola, J. C. (1996). Population dynamics, reproduction, growth, and secondary production of the mud-snail *Hydrobia ulvae* (Pennant). *Journal of Experimental Marine Biology and Ecology* **205**, 49–62. doi:10.1016/S0022-0981(96)02597-X

Sumikawa, S. (1994). Sex and reproduction. In 'Handbook of Malacology'. (Eds T. Habe, T. Okutani and S. Nishiwaki.) pp. 159–199. (Saientisutosha: Tokyo, Japan.) [In Japanese.]

Tashiro, M., Tomiyama, K., and Morino, H. (2001). Distribution of the brackish water snail, *Assiminea japonica* Martens (Gastropoda: Assimineidae) along Hinuma water system, middle Japan, with a comparison of population structure between observation sites. *Venus (Journal of the Malacological Society of Japan)* **60**, 79–91. [In Japanese.]

Wada, K., Nishihira, M., Furota, T., Nojima, S., Yamanishi, R., *et al.* (1996). The present status of benthic organisms inhabiting the tidal flats in Japan. *WWF Japan Science Report* **3**, 1–182. [In Japanese.]

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A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses

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Abstract

Gastropod egg masses are often deposited in the intertidal zone, where they are exposed to variable and often stressful environmental conditions that may affect the encapsulated embryonic development and survival of offspring. The present paper reviews data on developmental variation in gastropod egg masses owing to temperature, salinity, ultraviolet radiation (UVR) and oxygen availability. In general, increases in temperature or oxygen availability accelerate development, whereas UVR or extremes of salinity and temperature slow development and/or increase embryonic mortality. The relationships among these factors are discussed, as are their interactions with biotic factors, such as fouling, embryonic position within the egg mass and predation. One purpose of the present review is to raise awareness of these interactions so they become a focus for future research. Protective mechanisms of egg masses against environmental stresses are also reviewed.

Additional keywords: mollusc, oxygen availability, reproduction, salinity, temperature, ultraviolet radiation.

Introduction

Intertidal organisms face a variety of selective challenges while reproducing. They must protect their offspring against the environmental extremes of the intertidal zone, as well as against risks of predation and infection. Many gastropods have adapted to these challenges by laying their eggs in benthic masses. Although gastropod egg masses include a striking array of varied structures, they can be divided into two general categories: capsular and gelatinous, as defined below (see Figs 1,2).

Benthic egg masses are believed to provide protection to the developing embryos from environmental stresses and predation (Thorson 1950; Pechenik 1979; Strathmann 1985). Nevertheless, environmental factors still affect embryonic development, sometimes deleteriously. Gastropod intracapsular embryonic development and mortality may be influenced by temperature, salinity, ultraviolet radiation (UVR), oxygen availability, water flow, fouling, embryonic position, predation and parental history. These factors do not usually operate independently (Fig. 3) and, consequently, confounding relationships should be considered when studying embryonic development within gastropod egg masses. Once it is known how embryos react to certain environmental factors, it may be possible to predict their response to the associated local and global environmental events, such as thermal fluctuations and the thinning ozone layer.

Previous reviews have been written about gastropod egg masses, but discussion relating to benthic egg masses is typically ancillary to theoretical discussion of general reproductive patterns (e.g. Thorson 1950; Gallardo and Perron 1982). Other reviews cover potential protective mechanisms of egg masses, but they do not focus on the effects of environmental stresses on the embryos within (e.g. Pechenik 1979; Eyster 1986; Rawlings 1999). Still other reviews on gastropod egg masses are confined to one geographic region (e.g.

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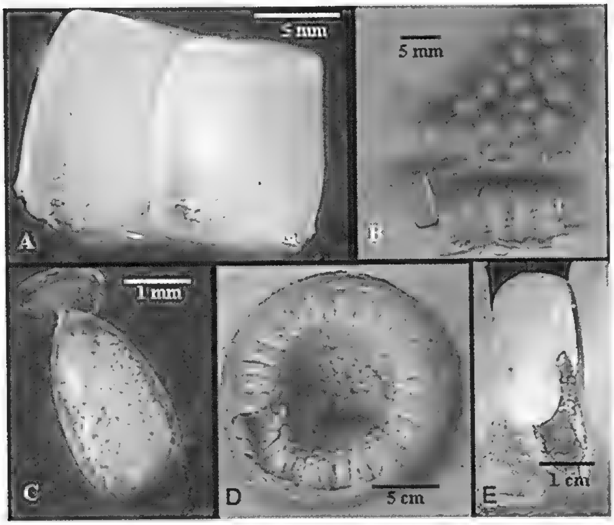

Fig. 1. Morphological variation in capsular caenogastropod egg masses collected along the Illawarra coastline, NSW. (*a*) *Dicathais orbita* capsules with swimming veligers. (*b*) Part of *Ranella australasia* egg mass. (*c*) *Mitra carbonaria* capsule containing trocophores. (*d*) Intact *Cabestena spenglerii* egg mass consisting of numerous capsules removed from brooding adult. (*e*) *C. spenglerii* capsule with only a few discrete eggs. The rest of the eggs have degenerated into a solid mass near the top of the capsule following exposure to sunlight.

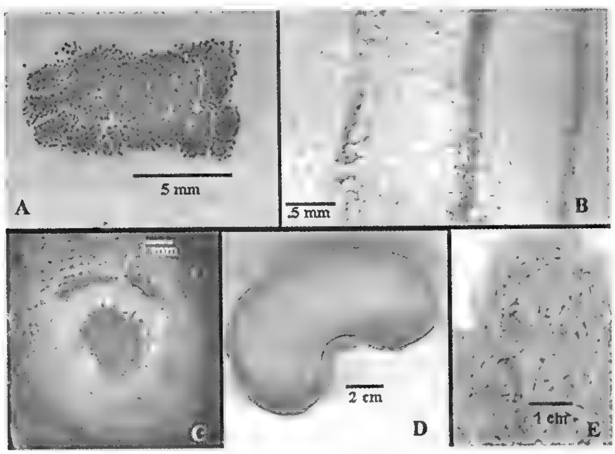

Fig. 2. Gelatinous egg masses collected along the Illawarra coastline, NSW. (*a*) *Bembicium nanum* egg mass with varying embryonic development. Peripheral embryos are more developed than central embryos as evidenced by their darker more developed shells. (*b*) *Dolabrifera brazieri* egg mass with veligers. (*c*) *Rostanga arbutus* egg mass with undeveloped eggs. (*d*) *Polinices (Conuber)* spp. egg mass. (*e*) *Dolabella auricularia* egg mass.

Strathmann 1987). Upon examination of the literature, very few studies were found that considered more than one environmental factor at a time (Table 1). Thus, there is a fundamental gap in our understanding of how confounding or interdependent environmental factors influence embryonic development in gastropod egg masses. The primary purpose of the present review is to consolidate available research about abiotic effects on gastropod egg mass development and to examine the complex relationships between abiotic factors, embryonic development and biotic factors, such as predation, fouling and embryonic position. It is hoped that this will help promote and guide future multifactorial research on embryonic development and mortality.

Egg mass structure and phylogeny

Because the structure and composition of egg masses are related to their phylogeny, it is necessary to clarify the taxonomic stance adopted in the present paper. In this review, gastropod classification will follow Beesley *et al.* (1998) (Table 2). Capsular egg masses are found among the Neritopsina and some Caenogastropoda (Fig. 1; Table 2). Gelatinous

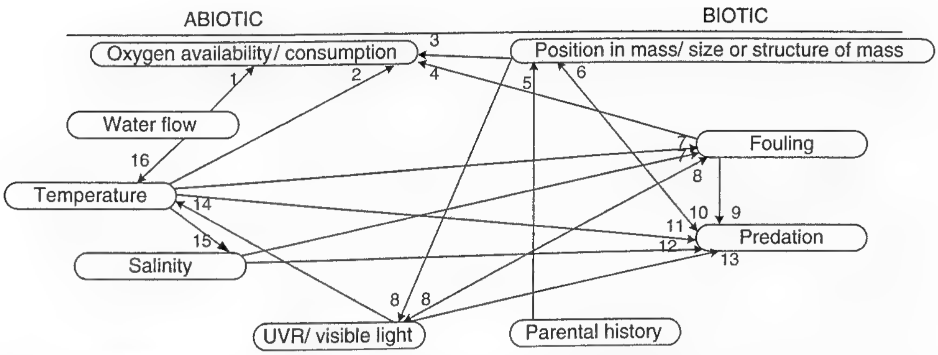

Fig. 3. Interactions of abiotic and biotic variables that can affect embryonic development within gastropod egg masses. The relationships illustrated are by no means ubiquitous or exhaustive. Rather, each arrow represents a potential relationship that has been identified in at least one study: 1, Kranenbarg *et al.* (2001); 2, Woods (1999); 3, Chaffee and Strathmann (1984); 4, Cohen and Strathmann (1996); Clark and Goetzfried (1978); 5, personal observation; 7, Lee and Kim (2002); 8, Biermann *et al.* 1992; 9, Laudien and Wahl (1999); 10, Rawlings (1990); 11, Sanford (1999); 12, McClanahan (1992); 13, Williamson *et al.* (1999); 14, Wissmann (2003); 15, personal observation; 16, Sabo *et al.* (1999). A single arrow indicates a relationship in which one variable affects the other. A double arrow indicates a relationship in which both variables affect each other.

masses are found among the Heterobranchia (Fig. 2*b–d*) and among some Caenogastropoda (Fig. 2*a*,*d*; Table 2). Some vetigastropods encase their eggs in jelly masses, although these often lack the organisation of heterobranch egg masses (Hickman 1992).

Capsular egg masses of many caenogastropods consist of multiple distinct capsules often connected to one another by a common basal layer (Fig. 1*b*,*d*). The often tough leathery capsule wall characteristic of neogastropods is composed of several structurally and chemically distinct layers (Tamarin and Carriker 1967; LeBoeuf 1971), sometimes sealed with an apical plug (Sullivan and Bonar 1985). Eggs and embryos are located inside the capsule walls, where they develop within intracapsular fluid (Bayne 1968). Some species use non-viable eggs called nurse eggs to nourish developing embryos (Gallardo and Perron 1982; Hoagland 1986). Neritid capsules have a calcareous apical capsule wall made with particles from a specialised crystal sac (D'Asaro 1986) and, thus, differ from caenogastropod egg capsules. Despite the fact that *Nerita atramentosa* is one of the most common snails on the rocky shore of south-eastern Australia, there is no published research to date examining the effects of environmental stresses on embryos of neritid egg capsules. Regrettably, they will not be discussed any further in the present review other than to note that such research would be interesting because neritid capsules are often deposited high on the shore (R. Przeslawski, personal observations).

Gelatinous egg masses consist of a jelly matrix in which many eggs are embedded (Fig. 2). A microscopic vitelline capsule surrounds each egg or small group of eggs (Eyster 1986; Klussmann-Kolb and Wägele 2001; Fig. 2). Some species lay egg masses that are a variation on the typical gelatinous egg mass structure. Naticid sand collars, for example, comprise adherent sand grains in addition to a gelatinous matrix in which microscopic capsules and embryos are embedded (Giglioli 1955). Other taxa, such as some Amphibolids, also incorporate relatively large amounts of sand into their egg masses (Benkendorff 1999; Pechenik *et al.* 2003). Unlike capsular masses, gelatinous masses ensure that embryos are isolated from other embryos within a mass by their surrounding

Table 1. Experiments on the developmental effects of various factors on encapsulated marine gastropod development

Reference	n	Abiotic					Biotic		
		Temperature	Salinity	UV	O_2/flow	Position	Foul	Parental history	Predation
Ganaros (1958)	1	x							
Thompson (1958)	1	x							
Scheltema (1965)	1		x						
Scheltema (1967)	1	x							
Hagerman (1970)	1								
Spight (1975)	1	x							
Switzer-Dunlap and Hadfield (1977)	4	x							
Pechenik (1978)	2				x				
Dehnel and Kong (1979)	1	x							
Pechenik (1982)	3		x						
Pechenik (1983)	1		x						
Chaffee and Strathmann (1984)	2								
Rose (1986)	1	x	x						
Roller and Stickle (1989)	1	x	x						
Rawlings (1990)	1								x
Rodriguez *et al.* (1991)	1	x							
Biermann *et al.* (1992)	1			x		x	x		
Palmer (1994)	1	x							
Booth (1995)	1				x	x			
Strathmann and Strathmann (1995)	3				x	x			
Cohen and Strathmann (1996)	2			x	x	x	x		
Rawlings (1996)	1			x					
Richmond and Woodin (1996)	1		x						
Woods and DeSilets (1997)	1		x						
Carefoot *et al.* (1998)	1			x					
Podolsky *et al.* (1998)	1	x							
Cancino *et al.* (2000)	1				x				
Podolsky (2000)	1	x							
Pechenik *et al.* (2003)	1	x	x		x				
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n, Number of mollusc species studied; position, embryonic position; foul, algal or microfaunal fouling; history, parental history. An 'x' denotes a variable examined in the listed study.

Table 2. Orthogastropod classification system and corresponding egg mass type that occurs in at least some species within each group (Beesley *et al.* 1998)

First tier of classification is superorder followed by order/superfamily and family. Species listed are representative of some egg masses commonly found in south-east Australia (Benkendorff 1999; R. Przeslawski, personal observations)

Taxa	Egg mass type	SE NSW representative species
Vetigastropoda		
Trochoidea	Gelatinous, capsules[1]	
Neritopsina		
Neritoidea	Capsule	*Nerita atramentosa*
Caenogastropoda		
Sorbeoconchia		
Campaniloidea	Gelatinous	
Cerithioidea	Gelatinous, capsules[2]	
Hypogastropoda		
Littorinimorpha	Gelatinous, capsule	*Bembicium nanum*, *Cabestana spengleri*
Neogastropoda	Capsule	*Dicathais orbita*, *Mitra carbonaria*
Heterobranchia		
Architectonicoidea	Gelatinous	
Pyramidelloidea	Gelatinous	
Rissoelloidea	Capsule	
Cephalaspidea	Gelatinous	*Bullina lineata*, *Hydatina physis*
Sacoglossa	Gelatinous	*Oxynoe viridis*, *Elysia australis*
Anaspidea	Gelatinous	*Aplysia* sp., *Bursatella leachii*
Notaspidea	Gelatinous	*Pleurobranchus* sp., *Berthellina citrina*
Thecosomata	Gelatinous	
Gymnosomata	Gelatinous	
Nudibranchia	Gelatinous	
Doridina	Gelatinous	*Dendrodoris nigra*, *Rostanga arbutus*
Dendronotina	Gelatinous	*Melibe australis*
Arminina	Gelatinous	
Aeolidina	Gelatinous	*Austraeolis ornata*, *Spurilla macleayi*
Basommatophora	Gelatinous	*Siphonaria* sp., *Salinator* sp.

[1]Trochoideans have various modes of reproduction; only a few species lay benthic egg masses (Hickman 1992).

[2]Some species of Cerithioidea are viviparous.

vitelline capsule. It is likely that many embryos receive their nutrition from intracapsular fluid (Moran 1999), whereas others receive nutrition from yolk granules or sacs associated with the egg mass (Clark and Goetzfried 1978; Williams 1980; Boucher 1983).

Among gastropod egg masses, considerable variation can occur in the number of eggs per capsule (Grant 1983; Strathmann 1985), egg and embryo size (Strathmann 1977; Christiansen and Fenchel 1979) and colour (D'Asaro 1966; Switzer-Dunlap and Hadfield 1977), as well as the shape and size of the egg mass (Hurst 1967; Chambers and McQuaid 1994). Although at least some of this variation occurs among individuals of the same species (Eyster 1979), there are only a very few studies that examine how much of this variation is due to environmental effects (e.g. Thompson 1958; Hagerman 1970; Cheung 1997). Thus, it can be difficult to determine the difference between intrinsic variation and environmental effects on gastropod egg masses. The present review considers variation in embryonic development.

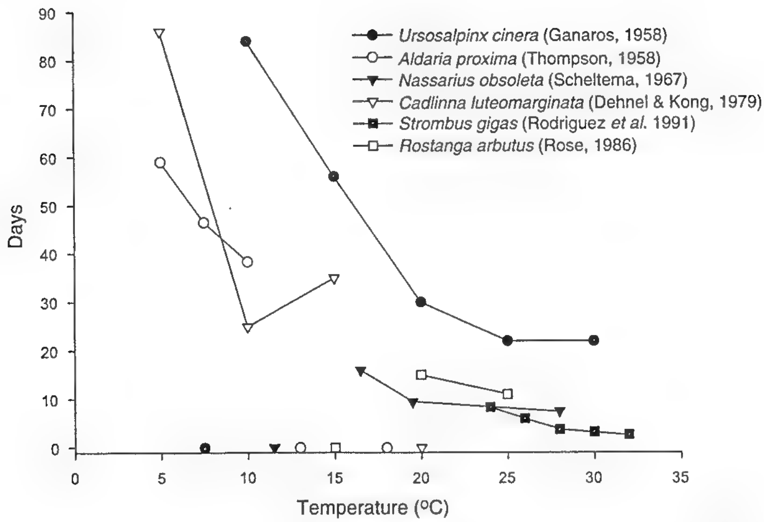

Fig. 4. The effects of temperature on developmental rate in benthic gastropod egg masses according to available literature. Unconnected symbols resting on the *x*-axis represent egg masses that did not hatch at the specified temperature. At 10°C, *Urosalpinx cinera* took longer than the experimental period of 84 days to hatch. The values for *Strombus gigas* were obtained using calculations performed by Rodriguez *et al.* (1991) as they did not present raw data.

Terminology

For clarity and consistency, 'egg' will refer to anything before the blastomere stage, including unfertilised eggs. Developing young will be referred to as 'embryos' until they leave the capsule (Giese and Pearse 1974). As accepted in most previous research, 'capsule' will describe both the rigid layered wall in capsular masses, as well as the vitelline membrane surrounding embryos in gelatinous egg masses. 'Egg mass' will refer to the entire discrete gelatinous mass or capsule group in one site. In the case of species that lay among spawning aggregations (e.g. many *Aplysia* or neogastropods), this definition could include ribbons or capsules from several individuals deposited in the same mass. 'Dead' and 'dying embryos' will include seriously deformed immobile embryos and embryos showing tissue damage or loose debris within an internal capsule (Woods and DeSilets 1997; Fig. 1*e*).

Temperature

Within tolerable temperature ranges for each species, the encapsulation period generally decreases as temperature increases for many invertebrates (Rothlisberg 1979; Boucher 1983; Rumrill 1990), including molluscs (Kress 1975; O'Dor *et al.* 1982; Palmer 1994; Caveriviere *et al.* 1999; Fig. 4). For gastropod embryos within capsular egg masses, it has even been suggested that hatching time can be estimated knowing only the taxon and the temperature (Spight 1975; Palmer 1994). This, however, assumes that all other variables discussed in the present paper are static or do not significantly affect the embryonic developmental rate. In addition, predicting hatching time based solely on taxon and temperature may be problematic owing to potential geographic or temporal variation in temperature compensation. This has been observed, for example, in the muricid *Nucella*

emarginata (Deshayes, 1839), with Alaskan populations hatching in significantly less time at temperatures 10°C lower than British Columbian populations (Palmer 1994).

Embryos become stressed and often die if exposed to extreme temperatures relative to their natural environment (Fig. 4) and seem more vulnerable to temperature extremes than adults. Thompson (1958), for example, found that the adult nudibranch *Adalaria proxima* (Alder & Hancock, 1854) spawned and remained healthy at a relatively high 13°C, but this temperature was lethal to eggs. Despite vulnerability to both high and low temperature extremes (Fig. 4), gastropod embryos may be more tolerant of lower temperatures within their range than higher temperatures. Struhsaker and Costlow (1969) found that planktotrophic larvae of *Littorina picta* had a high survival rate at temperatures lower than their established optimal developmental temperatures, but the larvae had lower survival rates at temperatures higher than optimal conditions. Similar observations have been made on encapsulated gastropod embryos. For example, Dehnel and Kong (1979) examined the effects of temperature on the egg masses of the nudibranch *Cadlinna luteomarginata* (MacFarland, 1966) along the coast of British Columbia and found the hatching time was fourfold faster at 15°C than at 5°C, although there was no difference in overall hatching success. However, at 20°C, the average summer temperature, embryos degenerated by the fourth cleavage stage (Fig. 4). Thus, the embryos of this species seemed much more tolerant of lower temperatures than higher temperatures within their natural thermal range, but because the egg masses used in the study were collected in winter, it is possible that they were better adapted to cold than those laid in the summer. Indeed, Dehnel and Kong (1979) do not specify whether this population even lays in the summer months or whether the egg masses persist into the spring and summer. Nevertheless, my own preliminary observations on south-eastern Australian gastropods are consistent with the suggestion that embryos of both gelatinous and capsular egg masses are more tolerant of low than high temperature extremes.

Although there is a lethal low and high temperature for gastropod embryos (Fig. 4), some embryos are able to protect against high temperatures to a certain extent. Recent research has revealed the presence of heat shock proteins inside the gelatinous egg masses of the cephalaspid *Melanochlamys diomedea* (Bergh, 1894) (Podolsky and Hoffmann 1998; Podolsky 2000). These proteins allow embryos to withstand high temperatures, such as those reached during low tide on a summer day, by preventing the degradation of proteins during heat stress and facilitating the refolding of proteins. These thermally protective proteins develop as the embryos mature (Podolsky and Hoffmann 1998). Thus, undeveloped embryos are especially vulnerable to high temperatures and they become less vulnerable to temperature extremes as they develop (Thorson 1950). It is presently unknown whether egg masses of other species contain thermally protective proteins.

Low temperatures can affect embryonic development by prolonging or halting it. Scheltema (1967) found that the embryonic development of the neogastropod *Ilyanassa obsoleta* (Say, 1822) slowed significantly as the temperature dropped (Fig. 4). The embryos ceased development at the lower threshold of the species' temperature range. However, these embryos remained viable for up to 9 weeks of exposure and continued development when returned to their normal temperature. Similarly, Ganaros (1958) found that embryos of the muricid *Urosalpinx cinerea* (Say, 1822) remained viable after being subjected to sub-freezing temperatures and, if only exposed for a short period, they recovered and developed fully. However, the embryonic mortality rate increased as exposure time to cold water increased. No similar studies have been conducted on embryos of gelatinous egg masses.

Strathmann and Chaffee (1984) point out that lower temperatures decrease embryonic metabolic rates, thus resulting in slower development. In addition, they suggest that lower temperatures could decrease intracapsular fluid viscosity and diffusion rates, thereby decreasing oxygen availability to the embryos (Fig. 3). However, as metabolic rate slows, the demand for oxygen will also decrease; thus, the effects of less oxygen availability may be negligible in light of lower embryonic metabolism. Further research is needed to determine causes and effects of changes in oxygen availability, temperature, metabolic rates and developmental rates, because these are likely to be interdependent factors.

The available literature presents dissenting views about whether temperature is the primary developmental regulator in certain gastropod populations. It has been suggested that although temperature often influences the speed of development, oxygen availability is the primary factor controlling the encapsulated development of embryos (Cancino *et al.* 2003). Furthermore, Clarke (1982) notes that many Antarctic marine invertebrates have very slow embryonic development, but suggests that this is not necessarily due to the extreme low temperatures. Rather, molluscs that have evolved in the Antarctic show temperature compensation and should not be subject to slow embryonic developmental rates due to low temperatures. Clarke (1982) suggests that, instead, it is the large egg size that results in the slow development of Antarctic invertebrate embryos. However, it is difficult to examine separately the effects of low temperature and large egg size in the field in polar regions because they often occur concurrently. In contrast, other studies suggest that temperature is the primary variable that controls the embryonic developmental rate (Spight 1975; Hoegh-Guldberg and Pearse 1995). It is unlikely that the relationship between temperature and egg size will be resolved until comparative experimental research is conducted, preferably on a species capable of producing eggs of different sizes (e.g. Jones *et al.* 1996) or a broad range of species with the same larval hatching type that produce eggs of different sizes (Clark and Goetzfried 1978).

Despite the obvious effect of temperature on gastropod developmental rate, some researchers fail to present adequate temperature data when reporting hatching times of egg masses (e.g. Govindan and Natarajan 1974; Pilkington 1974; Creese 1980). If the temperature is unknown, the developmental rate data are essentially useless. Therefore, it is imperative that all researchers reporting hatching times of gastropod egg masses monitor or control the temperature (e.g. Hurst 1967; Rose 1985; Chung *et al.* 2002).

Temperature is bound to several other abiotic and biotic factors that affect gastropod embryonic development (Fig. 3). First, the seawater temperature of intertidal pools or other still water is higher in sunlight than in shade. Therefore, it can become difficult to separate the effects of UVR and temperature in the field. The effects of UVR and sunlight on temperature are easily controlled in an artificial seawater system where temperature can be kept independent of light. Furthermore, UVR and temperature significantly interact to cause coral zooxanthellae expulsion (Wissmann 2003), as well as to affect the growth of intertidal algae (Hoffmann *et al.* 2003). No such studies examining the potentially synergistic effects of temperature and UVR have been conducted on gastropod egg masses.

The position of embryos within a mass may also influence their reaction to temperature stress. Embryos in the centre of a large mass are better protected from short-term environmental changes than embryos located peripherally (Strathmann and Hess 1999). In addition, temperature may directly affect predation (Sanford 1999) and microalgal fouling (Lee and Kim 2002). Furthermore, embryonic tolerance to temperature may be linked to salinity (Pechenik *et al.* 2003). Rose (1986) found that embryos of the nudibranch *Rostanga arbutus* (Angas, 1864) show the widest temperature tolerance at an intermediate salinity of

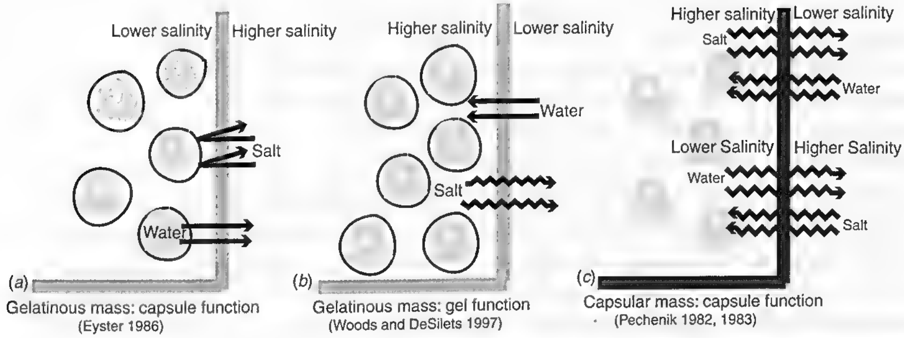

Fig. 5. The embryonic protection afforded by capsular and gelatinous egg mass structures to changes in salinty. A zig-zag line means the rate of movement is decreased, but the overall magnitude of change is slight. Mechanisms illustrated are based on research from listed references. (*a*) Function of vitelline capsules within gelatinous egg masses. (*b*) Function of gelatinous matrix. (*c*) Function of capsule walls in neogastropod egg masses.

34 p.p.t. Finally, higher temperatures have been associated with increased oxygen availability and consumption within egg masses (Roller and Stickle 1989; Woods 1999). All these factors should be considered when examining the effects of temperature on gastropod embryonic development.

Salinity

As with temperature, salinity extremes can affect embryonic mortality in egg masses. As salinity deviates from that within a species' normal habitat, the mortality of gastropod embryos increases (Struhsaker and Costlow 1969; Pechenik 1982; Woods and DeSilets 1997). However, as embryos develop they seem to become more tolerant to a wider range of salinities (Struhsaker and Costlow 1969; Pechenik 1983; Richmond and Woodin 1996). Thus, developing embryos vulnerable to salinity changes may require the protection of the egg capsule or associated gel matrix. Scheltema (1965) did not notice any significant differences between the levels of salinity that proved lethal to adults and hatched veligers of *Ilyanassa obsoleta*. It is possible that embryos of some species, particularly those in estuarine habitats, like *I. obsoleta*, use the protection of an egg capsule against salinity changes only during early development. Unfortunately, there is no comparable research among gelatinous egg masses and further research comparing the response of embryos, juveniles and adults is needed for both capsular and gelatinous egg masses.

Embryos within gelatinous egg masses do seem to be protected to some degree against salinity changes by both their vitelline capsules and the gelatinous matrix. In a detailed study of nudibranch capsules, Eyster (1986) examined the vitelline capsule structure in relation to salinity. She found that the capsule walls inhibit the passage of large molecules, including salts (Fig. 5*a*). She also noted that the capsules retain full structural integrity for the duration of encapsulation. However, embryos within the capsules were still vulnerable to high salinities owing to water efflux (Fig. 5*a*). Woods and DeSilets (1997) conducted similar experiments on the gelatinous matrix of *Melanochlamys diomedea* egg masses collected in areas subjected to periodic freshwater influx. They separated some embryonic capsules from the surrounding gel and exposed these to various test salinities. The gel improved survival only in very low salinity conditions by slowing the rate of salt efflux (Fig. 5*b*). The embryos themselves were equally tolerant to high salinities, regardless of the

presence of surrounding gel. Pechenik *et al.* (2003) similarly found that the embryos of the estuarine pulmonate *Amphibola crenata* (Gmelin 1791) were tolerant to extremely low salinities. The gelatinous egg collar itself showed no protective function to salinity changes, but tolerance was a property of the surrounding egg capsule or the embryos themselves. Further research examining both vitelline capsules and gelatinous matrices would likely reveal a combined protection of embryos against salinity changes that varied among species. These studies would be worthwhile on species that lay their egg masses in small intertidal pools, where salinity can reach high levels during low tide. Egg masses of such species may provide more effective protection against high salinities rather than low salinities. Indeed, a study comparing species that spawn in potentially high-salinity environments with estuarine species may reveal interesting adaptive differences to the extremes of low and high salinity.

In contrast with vitelline capsules within gelatinous masses, the much larger leathery capsules of some neogastropods are permeable to both NaCl and water, although this permeability may vary among species within a genus (Pechenik 1982; Fig. 5*c*). Despite this apparent lack of protection against salinity changes, encapsulated embryos were found to have a significantly higher tolerance to salinity changes than embryos removed prematurely from the egg capsule (Pechenik 1983). Thus, the higher tolerance of encapsulated embryos to salinity stress is likely a result of capsule wall function. The capsules probably reduce the rate of salinity change, despite not protecting against the magnitude of change (Pechenik 1982, 1983). So far, these studies have been restricted to the genus *Nucella* (Table 2). Research on different species would provide a more general understanding of the role of neogastropod egg capsules in providing protection from salinity fluctuations. Furthermore, the potential function of intracapsular fluid and other capsular contents in protection against changes in salinity remains unexplored.

In addition to embryonic mortality, salinity may also affect developmental rate. Rose (1986) observed that *Rostanga arbutus* embryos reared in 40 p.p.t. seawater developed more slowly than embryos reared in 34 p.p.t. seawater at the same temperature. Low salinities have also been shown to prolong embryonic development in other opisthobranchs, the sacoglossan *Elysia viridis* (Montagu, 1804) (Hagerman 1970) and three species of *Doto* (Kress 1975). Reasons for this are unknown, but may be due to the association between salinity and embryonic oxygen consumption rates, although this has only been documented on capsular egg masses (Roller and Stickle 1989).

Salinity is directly affected by temperature, with higher temperatures often leading to increased salinity through evapouration in small intertidal pools (R. Przeslawski, personal observations). Salinity itself affects some biotic factors that can influence gastropod embryonic development (Fig. 3). Salinity can influence the abundance and diversity of predators. As salinity deviates from normal conditions in a particular environment, the number of predators can decrease (McClanahan 1992). Similarly, salinity can affect the abundance and diversity of potential fouling microorganisms (Kocak and Kucuksezgin 2000; Lee and Kim 2002). Moreover, temperature may influence the effect of salinity changes on embryos. For example, Pechenik *et al.* (2003) found a significant interaction between salinity and temperature on the developmental rate and hatching success of *Amphibola crenata.*

Ultraviolet radiation

Ultraviolet radiation, especially UV-B, is deleterious to many organisms (Karanas *et al.* 1981; Wood 1987; Bothwell *et al.* 1994). Among gastropod egg masses, exposure to UVR

can stunt development, produce deformities and cause death (Biermann *et al.* 1992; Rawlings 1996; Carefoot *et al.* 1998). The severity of the effects of UVR may depend upon the age of the embryos. Biermann *et al.* (1992) exposed fresh and mature egg masses of the nudibranch *Archidoris montereyensis* (MacFarland, 1966) to sunlight and found the rates of embryonic mortality and deformity were significantly less in the mature egg ribbons. However, the previous history of the mature egg masses was unknown. It is therefore possible other variables contributed to the mortality difference among fresh and mature egg masses. Although the developmental risk is probably greatest during cleavage and early embryo development, UVR still poses a serious risk to embryos for the duration of their encapsulation.

The most logical protection against UVR exposure is for the adults to lay egg masses under boulders or in other areas shielded from sunlight. Spawning under boulders may also protect egg masses against desiccation, predation and high temperatures. Benkendorff and Davis (2002) have found that over half the molluscs depositing egg masses on intertidal reefs around Wollongong (NSW, Australia) exclusively attached them to the undersides of boulders. Other taxa occasionally lay in areas exposed to UVR, such as *Aplysia* species (Przeslawski *et al.* 2004). Indeed, certain molluscs, such as some *Siphonaria* species, lay exclusively in habitats exposed to full sunlight (Creese 1980; Benkendorff and Davis 2002). The vulnerability to and protection against UVR of certain amphibians is species specific (Blaustein *et al.* 1994), and even population specific (Belden and Blaustein 2002). Recent work among gastropod egg masses has also revealed species-specific UVR vulnerability. Przeslawski *et al.* (2004) have found that egg masses of species that lay exclusively in shaded habitats are very vulnerable to the harmful effects of UVR, whereas those that lay consistently in UVR-exposed habitats are not.

It has been suggested that species that regularly lay in UVR-exposed environments possess structural or chemical protection against UVR (Biermann *et al.* 1992). One possibility is that the egg masses are biochemically protected through UV-absorbing compounds. Ultraviolet-radiation-absorbing compounds, such as mycosporine-like amino acids (MAAs), have been identified recently in many marine organisms (reviewed by Shick and Dunlap 2002), including pelagic invertebrate eggs (Epel *et al.* 1999). It is generally accepted that marine animals obtain these MAAs from their diet or symbiosis with algae because animals lack the biochemical pathway to synthesise MAAs (Stochaj *et al.* 1994; Mason *et al.* 1998; Shick *et al.* 1999). With only a few exceptions discussed below, it is unknown whether gastropod egg masses contain UV-absorbing compounds.

To date, no MAAs or other UV-absorbing compounds have been found in capsular egg masses, although only those of the neogastoprods *Trophon* cf. *geversianus* (Pallas, 1774) and *Nucella emarginata* have been examined (Karentz *et al.* 1991; Rawlings 1996). Karentz *et al.* (1991) surveyed a broad range of marine Antarctic organisms, including a capsular egg mass from the neogastropod *Trophon* cf. *geversianus* and a gelatinous egg ribbon from the vetigastropod *Margarella antarctica* (Lamy, 1905), and found that 90% of all organisms contained MAAs. Whereas most organisms contained a substantial concentration of a variety of MAAs, the two gastropod egg masses examined showed little or no sign of MAAs, despite their presence in the adults. Unfortunately, the authors do not specify whether the egg masses were collected from shaded or sunny habitats. Rawlings (1996) attempted to extract MAAs from capsules of the neogastropod *Nucella emarginata*, but without success. However, only the capsule walls were tested for MAAs, not the intracapsular fluid or embryos. Rawlings (1996) did, however, conclusively show that the

outer capsule wall absorbed UVR, particularly UV-B. Thus, embryos within the leathery capsule may have no need for the additional protection of MAAs.

In contrast with the experiments mentioned above, Carefoot *et al.* (1998) found that the gelatinous egg masses of *Aplysia dactylomela* (Rang, 1828) were rich in MAAs, but adult diet determined their presence. *Aplysia* species lay their egg masses both under boulders and in areas exposed to sunlight, so the presence of MAAs may be an evolved protective mechanism rather than a coincidental dietary benefit. It would be worthwhile to conduct similar experiments on gastropods with different laying habitats, particularly those that lay exclusively in environments exposed to UVR, to determine whether the presence of MAA in egg masses is an evolved protection (Cockell and Knowland 1999).

The effects of UVR on gastropod egg masses are potentially confounded with several other factors (Fig. 3), such as the placement of embryos within the egg mass. In gelatinous egg masses, where the embryos have a fixed position, the surrounding gel and embryos near the top can act as a shield for the inner embryos (Biermann *et al.* 1992). In addition, the water depth at which the egg masses occur could influence UVR penetration. Significant amounts of UV-B can be transmitted through 5–10 m water, whereas biologically harmful UVR can penetrate more than 20 m below the surface (Karentz and Lutze 1990; Booth and Morrow 1997). The penetration of UVR in seawater also depends on water clarity and, thus, UVR and the transmission of visible light can vary among regions at a similar depths depending on the amount of sediment, phytoplankton and dissolved solutes (Shooter *et al.* 1998). Exposure to UVR can also be affected by surface fouling on the egg mass. Algal fouling is greater in sunlight and it has been suggested that such a covering over the egg mass could significantly shield the embryos within from UVR (Biermann *et al.* 1992). Like salinity and temperature, UVR and associated visible light directly affect microalgal fouling (Biermann *et al.* 1992) and predation (Williamson *et al.* 1999). As mentioned previously, UVR can also interact significantly with temperature (Hoffmann *et al.* 2003; Wissmann 2003) and the effects of this potential relationship need to be investigated on gastropod egg masses.

Oxygen availability

Oxygen availability can dramatically influence the development of embryos within egg masses. In a series of experiments, Strathmann and Strathmann (1995) demonstrated that oxygen limited embryonic development within gelatinous opisthobranch egg masses. They found that embryos of three species showed arrested development during hypoxia until they were returned to a normal oxygen level. Furthermore, lower oxygen availability throughout the development period reduced shell length at hatching. These observations have recently been supported in the capsular egg masses of *Chorus giganteus* (Lesson, 1829) (Cancino *et al.* 2003).

The direct effects of oxygen availability on gastropod embryo development are usually not studied independently but, rather, are used to explain the effects of other environmental factors. Oxygen availability within egg masses is inextricably linked to water flow, embryonic position within the egg mass and fouling (Fig. 3).

Among gelatinous egg masses, flowing water accelerates the rate of embryonic development by decreasing hatching time and increasing embryo activity (Eyster 1986) because it most likely increases the overall oxygen supply to the mass through diffusion (Strathmann and Hess 1999). Chaffee and Strathmann (1984) found that flowing water decreases asynchronous development within a spherical gelatinous mass, whereas still water promotes relatively high developmental variation. The same study found no effect of

still water on development among elongated gelatinous ribbons. Biermann *et al.* (1992) also found a significant interaction between water flow and egg mass thickness. There was no difference in embryonic developmental rates between egg ribbons maintained in still water and those exposed to a strong current; but, when the thin ribbons of the egg masses were layered, forming a thicker structure, there was a noticeable developmental retardation in still water. Therefore, it is likely that the shape of the egg mass determines, in part, the developmental effects of oxygen availability as controlled by water flow (Kranenbarg *et al.* 2001). There has been no similar research into the combined effects of oxygen availability, water flow and egg mass structure on the development of embryos within capsular egg masses.

The effects of desiccation on embryonic oxygen availability have not yet been studied in detail. Many intertidal gastropod egg masses can tolerate brief periods of desiccation (Strathmann 1987) and some species are desiccated daily in the intertidal zone during low tides (D'Asaro 1970; Benkendorff 1999; R. Przeslawski, personal observations). However, if the egg masses are allowed to dry out for more than several hours, the embryos within will die (Creese 1980; Spight 1977). The intertidal capsules of *Ilyanassa obsoleta* were no more effective protecting against desiccation than the capsules of a subtidal nassariid (Pechenik 1978). It is not known why certain egg masses are laid consistently in areas regularly subject to desiccation. Pechenik *et al.* (2003) found that pulmonate embryos in a sandy gelatinous egg mass hatched faster if they were exposed to air for a few hours a day and suggested that this reflected the greater oxygen availability in the air-exposed egg masses, although this has yet to be tested. If air exposure does, indeed, decrease the encapsulation period, then this may outweigh the potential risks associated with desiccation.

The placement of the embryos within the egg mass also influences embryonic oxygen availability. Many neogastropods deposit their egg capsules in a clump and the capsules near the periphery will generally develop faster than the central capsules (R. Przeslawski, personal observations). This trend is even more accentuated in gelatinous masses (Fig. 2*a*). Because embryos in a capsular mass are free to move within a relatively large chamber (D'Asaro 1986; Fig. 1), their position within the capsule changes constantly and oxygen supply is relatively uniform for most embryos within a capsule (Strathmann and Chaffee 1984). However, eggs and embryos of gelatinous masses are fixed in one location within the whole mass (Hurst 1967; Switzer-Dunlap and Hadfield 1977; Fig. 2). Embryos located within the central region of a gelatinous egg mass frequently show arrested or retarded development compared with embryos located peripherally (Chaffee and Strathmann 1984; Biermann *et al.* 1992; Lee and Strathmann 1998; Fig. 2*a*), which is associated with lower oxygen availability (Strathmann and Strathmann 1995). The egg masses of several species are normally hypoxic in central locations (Cohen and Strathmann 1996; Woods 1999). As a result, central embryos can be more developmentally dependent on environmental factors like water flow and algal fouling, whereas those at the periphery are more vulnerable to other environmental conditions, such as desiccation and extremes in temperature and salinity.

Although many selective pressures exist to reduce the period of encapsulation (Havenhand 1993), the benefits of the delayed development of centrally located embryos may outweigh the risks of slower development. A large egg mass with varying developmental rates can contribute to populations by releasing viable embryos from the mass over a period of days and even weeks (Gibson and Fu-Shiang 1994). With this bet-hedging strategy, veligers within one mass are exposed to a variety of conditions at

hatching. Chances for optimal conditions for at least some veligers are maximised. An extreme example of centrally retarded development is the naticid mud snail *Conuber sordidus* (Swainson, 1821), which lays its eggs in a large sausage-shaped jelly (Smith *et al.* 1989; Fig. 2*d*). Although the majority of the eggs are embedded near the outer surface, a large number of eggs exist throughout the entire mass. Because the egg mass is so large, the centrally located eggs are exposed to severe hypoxia and their development is arrested (Booth 1995). However, as the numerous peripheral embryos hatch, the gel surrounding them degrades and the oxygen available to the central region increases, enabling continued development of the internal embryos. Thus, a single egg mass can release viable veligers over a period of weeks depending on temperature (Booth 1995; R. Przeslawski, personal observations).

In addition to embryonic position, algal and microfaunal fouling can also have an effect on embryonic development by modifying oxygen availability. Algae alter the internal oxygen concentration of egg masses by producing oxygen in daylight and consuming oxygen at night (Strathmann 2000). By regulating the oxygen availability within egg masses, algal photosynthesis and metabolism may stabilise oxygen conditions in the egg mass, thereby controlling embryonic developmental rates (Cohen and Strathmann 1996). A study of amphibian eggs found that egg masses contained a green algae specific to amphibian eggs that increased oxygen availability to the embryos (Pinder and Friet 1994). No similar studies on potential symbiotic associations between algae and gastropod egg masses have been conducted.

Despite potential benefits to gastropod embryonic development, algae also promote protist and bacterial growth (Fogg 1983). Unlike algae, these organisms do not produce oxygen; in fact, they deplete available oxygen through respiration (Cohen and Strathmann 1996). Bacteria and fungi have been shown to be deleterious to gastropod larval development (Struhsaker and Costlow 1969, Biermann *et al.* 1992), although later developmental stages may be less susceptible (Struhsaker and Costlow 1969). It is not known whether the deleterious effects observed were due to hypoxia or to a byproduct of the fouling organisms. A more conclusive study was undertaken by Cancino *et al.* (2000), in which the oxygen availability to embryos of the muricid *Chorus giganteus* was reduced by sessile protozoa that fouled some egg capsules. The protozoa decreased oxygen tension and the embryos within fouled capsules not only had a much longer hatching time, but they also showed marked impairment of shell growth.

Certain egg masses are not vulnerable to heavy algal fouling owing to the laying behaviour of the adult. Because sunlight is necessary for algae to flourish, the risk of fouling is low when an egg mass is laid under boulders. Moreover, some egg masses hatch in a few days and are not heavily fouled owing to this short development period. It is not known whether gastropod egg masses contain any biochemical protection against algal fouling.

Similarly, gastropod egg masses may also provide protection against bacterial fouling and infection. Benkendorff *et al.* (2001) have reported antimicrobial properties in both capsular and gelatinous egg masses of 39 species of molluscs. In contrast, Pechenik *et al.* (1984) did not find any antibiotic properties in the intracapsular fluid of *Nucella lapillus* (Linnaeus, 1758) capsules, although this result should be interpreted cautiously because there were limitations in the methods used to test for antimicrobial activity (Benkendorff *et al.* 2000*a*). In addition, Pechenik *et al.* (1984) do not indicate the age of the capsules examined. Because chemical ripening has recently been found to occur in related species (Benkendorff *et al.* 2000*b*), active compounds may have decomposed in mature or stressed egg capsules.

Oxygen availability and consumption may also be interdependent with several abiotic factors (Fig. 3). Although oxygen availability is affected by temperature (Green and Carrit 1967), Cancino *et al.* (2003) found no significant interaction between temperature and oxygen availability on the encapsulated development of *Chorus giganteus*. Further research on capsular and gelatinous egg masses examining the potential relationship between oxygen availability and temperature would help clarify any interactions. Another study revealed a significant interaction between temperature and salinity on embryonic oxygen consumption (Roller and Stickle 1989). Temperature and salinity most likely affect oxygen consumption by affecting the health and metabolism of the embryos, as well as influencing the rates of oxygen diffusion.

Discussion

Gastropod egg masses are often exposed to a wide variety of environmental conditions in the intertidal regions in which they are commonly laid. These environmental factors affect embryonic development and mortality, but they are not themselves independent of each other. The present paper has reviewed abiotic factors affecting gastropod embryonic development and mortality: temperature, salinity, oxygen availability and UVR. In addition, relationships among these factors and their interactions with biotic factors were explored (Fig. 1).

Despite recent advances in our understanding of gastropod egg mass structure and development, there are still large gaps in our knowledge. First and foremost, fundamental structural and developmental data are still needed for the egg masses of many gastropods. Although North American and European species have been studied relatively frequently (e.g. Strathmann 1987) and several comprehensive studies have examined the egg mass structure of some Australasian taxa (Pilkington 1974; Rose 1985), details about the egg masses and embryos of many species remain unknown. In addition, possible egg mass or capsule changes over time have not been examined for most species. Without basic structural and developmental knowledge, there is no foundation for comparisons of the effects of environmental effects on egg mass development.

The majority of studies pertaining to environmental effects on gastropod egg mass development examine only one variable at a time (Table 1). There is, of course, nothing wrong with this approach and it can provide valuable information as long as other potential factors influencing development are controlled or are negligible. However, a multifactorial approach can reveal the relationships among factors that control embryonic development and mortality. This can be accomplished using various treatment combinations of two or more factors (e.g. Pechenik *et al.* 2003). Whenever possible, researchers should couple laboratory based experiments with field measurements of the factors examined and *in situ* developmental data of encapsulated gastropod embryos. This will ensure the relevance of laboratory studies and allow researchers to better interpret findings in the field.

Understanding the complex relationships among some of these factors will further our understanding of gastropod development in their natural environment. The present review has only discussed the potential effects of biotic variables on gastropod embryonic development in relation to their interactions with abiotic variables. There are still relatively few studies on the direct effects of biotic variables on gastropod egg mass development (Table 1), and future research should aim to clarify the interactions between abiotic and biotic factors that affect gastropod embryonic development (Fig. 3).

Comparisons of the developmental effects of various environmental factors on capsular and gelatinous masses are needed to better understand the differences among taxa regarding

vulnerability and possible protection of egg masses against harmful environmental factors (e.g. Przeslawski *et al.* 2004). Such studies could have interesting implications for evolutionary divergences of certain groups of gastropods through comparative examinations of structural adaptations of egg masses. Within the context of the present review, capsular egg masses were represented exclusively by caenogastropods, whereas gelatinous egg masses, with one exception (Booth 1995), were heterobranchs. Although egg mass structure and phylogeny are closely related, there are enough exceptions (see Table 2) so that future research should attempt to distinguish the effects of phylogeny from egg mass structure. Further comparative research on the effects of environmental stresses on gelatinous caenogastropod, capsular caenogastropod, and heterobranch egg masses may help separate the effects of environmental stresses based on phylogeny or structure.

Finally, further research on a range of species is necessary in order to determine possible relationships among various gastropod groups and populations. Struhsaker and Costlow (1969) state that the tolerance of embryos to changes in conditions like salinity may be contingent on the stability of the environment in which the adults are normally found. Thus, larvae in a subtidal tropical region with stable conditions would be expected to be less tolerant of environmental changes compared with larvae in an intertidal temperate region experiencing abrupt salinity and temperature changes. This hypothesis remains largely untested because researchers have yet to study empirically the effects of environmental stability on egg mass tolerance to environmental stresses. Such studies could provide valuable developmental information on a broad geographical range of species while identifying the vulnerabilities and tolerances of gastropod embryos.

Tolerance to environmental stress by encapsulated gastropod embryos may also depend on the zone of the shore in which they occur. Rawlings (1999) has suggested that intertidal egg masses may be no more effective in protecting against environmental stresses than subtidal egg masses, but this has yet to be tested. Studies comparing the developmental effects of environmental stresses between intertidal and subtidal egg masses may reveal habitat-specific adaptations important to intertidal ecological research. Regardless of the results, such studies would lead to examination of an evolutionary basis for intertidal spawning. For example, Spight (1977) found that *Thais lamellosa* showed no preference for intertidal spawning habitats, such as tidepools with reduced physical stresses, and that they often deposited their egg capsules in habitats where embryonic mortality was relatively high. Spight (1977) suggested that this may be due to higher site quality for other life stages, which outweighed the embryonic costs. Although several studies have explored the adaptations of egg masses to intertidal environmental stresses (reviewed by Pechenik 1978; Rawlings 1999), there is a severe lack of knowledge pertaining to the evolutionary advantages associated with egg mass deposition in this habitat. Species may deposit egg masses in the intertidal zone to minimise encapsulation period, reduce predation or fouling, or vary larval dispersal; however, this remains speculative. Survival advantages must exist to counteract the risks associated with spawning in such a physiologically hostile environment, but these are not necessarily the same for all taxa. With proper multifactorial experiments on a range of gastropod species, we can further understand the complex effects of intertidal environmental stresses on encapsulated gastropod development.

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References

Bayne, C. J. (1968). Histochemical studies on the egg capsules of eight gastropod molluscs. *Proceedings of the Malacological Society of London* **38**, 199–212.

Beesley, P. L., Ross, G. L. B., and Wells, A. (Eds) (1998). 'Mollusca: The Southern Synthesis. Fauna of Australia', Vol 5. (CSIRO Publishing: Melbourne, Australia.)

Belden, L. K., and Blaustein, A. R. (2002). Population differences in sensitivity to UV-B radiation for larval long-toed salamanders. *Ecology* **83**, 1586–1590.

Benkendorff, K. (1999). 'Bioactive Molluscan Resources and Their Conservation: Biological and Chemical Studies on the Egg Masses of Marine Molluscs.' PhD Thesis. (University of Wollongong: Wollongong, Australia.) http://www.library.uow.edu.au/adt-NWU/public/adt-NWU20011204.154039/index.html [Accessed March 2004]

Benkendorff, K., and Davis, A. R. (2002). Identifying hotspots of molluscan species richness on rocky intertidal reefs. *Biodiversity and Conservation* **11**, 1959–1973. doi:10.1023/A:1020886526259

Benkendorff, K., Davis, A. R., and Bremner, J. B. (2000*a*). Rapid screening methods for detecting antimicrobial activity in the egg masses of marine molluscs. *Journal of Medical and Applied Malacology* **10**, 211–223.

Benkendorff, K., Bremner, J., and Davis, A. (2000*b*). Tyrian purple precursors in the egg masses of the Australian muricid *Dicathais orbita*: a possible defensive role. *Journal of Chemical Ecology* **26**, 1037–1050. doi:10.1023/A:1005441116095

Benkendorff, K., Davis, A. R., and Bremner, J. B. (2001). Chemical defense in the egg masses of benthic invertebrates: an assessment of antibacterial activity in 39 mollusks and 4 polychaetes. *Journal of Invertebrate Pathology* **78**, 109–118. doi:10.1006/JIPA.2001.5047

Biermann, C., Schinner, G., and Strathmann, R. (1992). Influence of solar radiation, microalgal fouling, and current on deposition site and survival of embryos of a dorid nudibranch gastropod. *Marine Ecology Progress Series* **86**, 205–215.

Blaustein, A., Hoffman, P. D., Hokit, D. G., Kiesecker, J. M., Walls, S. C., and Hays, J. B. (1994). UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proceedings of the National Academy of Sciences USA* **91**, 1791–1795.

Booth, C. R., and Morrow, J. H. (1997). The penetration of UV into natural waters. *Photochemistry and Photobiology* **65**, 254–275.

Booth, D. T. (1995). Oxygen availability and embryonic development in sand snail *Polinices sordidus* egg masses. *Journal of Experimental Biology* **198**, 241–247.

Bothwell, M., Sherbot, D., and Pollock, C. (1994). Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science* **265**, 97–100.

Boucher, L. M. (1983). Extra-capsular yolk bodies in the egg masses of some tropical Opisthobranchia. *Journal of Molluscan Studies* **49**, 232–241.

Cancino, J. M., Gallardo, J. A., Torres, F., Leiva, G., and Navarro, J. M. (2000). Effects of sessile Protozoa on intracapsular oxygen tension and embryonic shell calcification in the muricid *Chorus giganteus*. *Marine Ecology Progress Series* **200**, 141–148.

Cancino, J. M., Gallardo, J. A., and Torres, F. A. (2003). Combined effects of dissolved oxygen concentration and water temperature on embryonic development and larval shell secretion in the marine snail *Chorus giganteus* (Gastropoda: Muricidae). *Marine Biology* **142**, 133–139.

Carefoot, T. H., Harris, M., Taylor, B. E., Donovan, D., and Karentz, D. (1998). Mycosporine-like amino acids: possible UV protection in eggs of the sea hare *Aplysia dactylomela*. *Marine Biology* **130**, 389–396. doi:10.1007/S002270050259

Caveriviere, A., Francois, D., and Diallo, A. (1999). Observations on the influence of temperature on the length of embryonic development in *Octopus vulgaris* (Senegal). *Aquatic Living Resources* **12**, 151–154. doi:10.1016/S0990-7440(99)80024-2

Chaffee, C., and Strathmann, R. R. (1984). Constraints on egg masses: 1. Retarded development within thick egg masses. *Journal of Experimental Marine Biology and Ecology* **84**, 73–83. doi:10.1016/0022-0981(84)90231-4

Chambers, R. J., and McQuaid, C. D. (1994). Notes on the taxonomy, spawn and larval development of South African species of the intertidal limpet *Siphonaria* Gastropoda: Pulmonata. *The Journal of Molluscan Studies* **60**, 263–275.

Cheung, S. G. (1997). Physiological and behavioural responses of the intertidal scavenging gastropod *Nassarius festivus* to salinity changes. *Marine Biology* **129**, 301–307. doi:10.1007/S002270050170

Christiansen, F. B., and Fenchel, T. M. (1979). Evolution of marine invertebrate reproductive patterns. *Theoretical Population Biology* **16**, 267–282.

Chung, E., Kim, S., Park, K., and Park, G. (2002). Sexual maturation, spawning, and deposition of the egg capsules of the female purple shell, *Rapana venosa* (Gastropoda: Muricidae). *Malacologia* **44**, 241–257.

Clark, K., and Goetzfried, A. (1978). Zoogeographic influences on development patterns of North Atlantic ascoglossa and nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies* **44**, 283–294.

Clarke, A. (1982). Temperature and embryonic development in polar marine invertebrates. *International Journal of Invertebrate Reproduction* **5**, 71–82.

Cockell, C. S., and Knowland, J. (1999). Ultraviolet radiation screening compounds. *Biological Review* **74**, 311–345. doi:10.1017/S0006323199005356

Cohen, S., and Strathmann, R. (1996). Embryos at the edge of tolerance: effects of environment and structure of egg masses on supply of oxygen to embryo. *The Biological Bulletin* **190**, 8–15.

Creese, R. G. (1980). Reproductive cycles and fecundities of two species of Siphonaria (Mollusca: Pulmonata) in South-eastern Australia. *Australian Journal of Marine and Freshwater Research* **31**, 37–47.

D'Asaro, C. N. (1966). The egg capsules, embryogenesis, and early organogenesis of a common oyster predator, *Thais haemastoma floridana* (Gastropoda: Prosobranchia). *Bulletin of Marine Science* **16**, 884–914.

D'Asaro, C. N. (1970). Egg capsules of some Prosobranchs from the Pacific coast of Panama. *The Veliger* **13**, 31–43.

D'Asaro, C. N. (1986). Laboratory spawning, egg membranes, and egg capsules of 14 small marine prosobranchs from Florida and Bimini, Bahamas. *American Malacological Bulletin* **4**, 185–199.

Dehnel, P. A., and Kong, D. C. (1979). The effect of temperature on developmental rates in the nudibranch *Cadlinna luteomarginalata. Canadian Journal of Zoology* **57**, 1835–1844.

Epel, D., Hemela, K., Shick, M., and Patton, C. (1999). Development in the floating world: defenses of eggs and embryos against damage from UVR. *American Zoologist* **39**, 271–278.

Eyster, L. (1979). Reproduction and development variability in the opisthobranch *Tenellia pallida. Marine Biology* **51**, 133–140.

Eyster, L. (1986). The embryonic capsules of nudibranch molluscs: literature review and new studies on albumen and capsule wall ultrastructure. *American Malacological Bulletin* **4**, 205–216.

Fogg, G. E. (1983). The ecological significance of extracellular products of phytoplankton photosynthesis. *Botanica Marina* **26**, 3–14.

Gallardo, C. S., and Perron, F. E. (1982). Evolutionary ecology of reproduction in marine benthic molluscs. *Malacologia* **22**, 109–114.

Ganaros, A. E. (1958). On development of early stages of *Urosalpinx cinerea* (Say) at constant temperatures and their tolerance to low temperatures. *Biological Bulletin* **114**, 188–195.

Gibson, G. D., and Fu-Shiang, C. (1994). A metamorphic inducer in the Opisthobranch *Haminea callidegenita*: partial purification and biological activity. *Biological Bulletin* **187**, 133–143.

Giese, A. C., and Pearse, J. S. (1974). Introduction and general principles. In 'Reproduction of Marine Invertebrates', Vol. 1. (Eds A. C. Giese and J. S. Pearse.) pp. 1–49. (Academic Press: New York, USA.)

Giglioli, M. E. C. (1955). The egg masses of the Naticidae (Gastropoda). *Journal of the Fisheries Research Board Canada* **12**, 287–327.

Govindan, K., and Natarajan, R. (1974). Studies on Neritidae from peninsular India. *Proceedings of the Indian National Science Academy Part B* **38**, 225–239.

Grant, A. (1983). Notes and comments on the evolution of brood protection in marine benthic invertebrates. *American Naturalist* **122**, 549–555. doi:10.1086/284155

Green, E., and Carrit, D. (1967). New tables for oxygen saturation of seawater. *Journal of Marine Research* **25**, 140–147.

Hagerman, L. (1970). The influence of low salinity on survival and spawning of *Elysia viridis* (Montagu) (Opisthobranchia, Sacoglossa). *Sarsia* **42**, 1–6.

Havenhand, J. (1993). Egg to juvenile period, generation time, and the evolution of larval type in marine invertebrates. *Marine Ecology Progress Series* **97**, 247–260.

Hickman, C. S. (1992). Reproduction and development of Trochacean gastropods. *The Veliger* **35**, 245–272.

Hoagland, K. E. (1986). Patterns of encapsulation and brooding in the Calyptraeidae (Prosobranchia: Mesogastropoda). *American Malacological Bulletin* **4**, 173–183.

Hoegh-Guldberg, O., and Pearse, J. (1995). Temperature, food availability, and the development of marine invertebrate larvae. *American Zoologist* **35**, 415–425.

Hoffmann, J., Hansen, L., and Klinger, T. (2003). Interactions between UV radiation and temperature limit inferences from single-factor experiments. *Journal of Phycology* **39**, 268–272.

Hurst, A. (1967). The egg masses and veligers of thirty northeast Pacific Opisthobranchs. *The Veliger* **9**, 255–288.

Jones, H., Todd, C., and Lambert, W. (1996). Intraspecific variation in embryonic and larval traits of the dorid nudibranch mollusk *Adalaria proxima* Alder and Hancock) around the northern coasts of the British Isles. *Journal of Experimental Marine Biology and Ecology* **202**, 29–47. doi:10.1016/0022-0981(96)00029-9

Karanas, J. J., Worrest, R. C., and Van Dyke, H. (1981). Impact of UV-B radiation on the fecundity of the copepod *Acartia clausii. Marine Biology* **65**, 125–133.

Karentz, D., and Lutze, L. (1990). Evaluation of biologically harmful ultraviolet radiation in Antarctica with a biological dosimeter designed for aquatic environments. *Limnology and Oceanography* **35**, 549–561.

Karentz, D., McEuen, F. S., Land, M. C., and Dunlap, W. C. (1991). Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Marine Biology* **108**, 157–166.

Klussmann-Kolb, A., and Wägele, H. (2001). On the fine structure of Opisthobranch egg masses (Mollusca, Gastropoda). *Zoologischer Anzeiger* **240**, 101–118.

Kocak, F., and Kucuksezgin, F. (2000). Sessile fouling organisms and environmental parameters in the marinas of the Turkish Aegean coast. *Indian Journal of Marine Sciences* **29**, 149–157.

Kranenbarg, S., Verhagen, J., Muller, M., and van Leeuwen, J. (2001). Consequences of forced convection for the constraints on size and shape in embryos. *Journal of Theoretical Biology* **212**, 521–533. doi:10.1006/JTBI.2001.2391

Kress, A. (1975). Observations during embryonic development in the genus *Doto* (Gastropoda, Opisthobranchia). *Journal of the Marine Biological Association of the United Kingdom* **55**, 691–701.

Laudien, J., and Wahl, M. (1999). Indirect effects of epibiosis on host mortality: Seastar predation on differently fouled mussels. *Marine Ecology Progress Series* **20**, 35–47. doi:10.1046/J.1439-0485.1999.00063.X

LeBoeuf, R. (1971). *Thais emarginata* (Deshayes): description of the veliger and egg capsule. *The Veliger* **14**, 205–211.

Lee, C. E., and Strathmann, R. R. (1998). Scaling of gelatinous clutches: effects of siblings' competition for oxygen on clutch size and parental investment per offspring. *American Naturalist* **151**, 293–310. doi:10.1086/286120

Lee, J. B., and Kim, B. Y. (2002). Growth characteristics of five microalgal species isolated from Jeju Island and four microalgal stock strains in hatchery. *Algae (Korean Phycological Society)* **17**, 117–125.

Mason, D. S., Schaefer, F., Shick, J. M., and Dunlap, W. C. (1998). Ultraviolet radiation absorbing mycosporine-like amino acids (MAAs) are acquired from their diet by medaka fish (*Oryzias latipes*) but not by SKH-1 hairless mice. *Comparative Biochemistry and Physiology* **120A**, 587–598.

McClanahan, T. R. (1992). Epibenthic gastropods of the Middle Florida Keys: the role of habitat and environmental stress on assemblage composition. *Journal of Experimental Marine Biology and Ecology* **160**, 169–190. doi:10.1016/0022-0981(92)90236-4

Moran, A. L. (1999). Intracapsular feeding by embryos of the gastropod genus Littorina. *Biological Bulletin* **196**, 229–240.

O'Dor, R. K., Balch, N., Foy, E. A., Hirtle, R. W. M., Johnston, D. A., and Amaratunga, T. (1982). Embryonic development of the squid, *Illex illecebrosus*, and effect of temperature on development rates. *Journal of Northwest Atlantic Fishery Science* **3**, 41–45.

Palmer, A. R. (1994). Temperature sensitivity, rate of development, and time to maturity: geographic variation in laboratory-reared *Nucella* and a cross-phyletic overview. In 'Reproduction and Development of Marine Invertebrates'. (Eds. W. H. Wilson Jr, S. A. Stricker and G. L. Shinn.) pp. 177–194. (Johns Hopkins University Press: Baltimore, MD, USA.)

Pechenik, J. (1978). Adaptations to intertidal development: studies on *Nassarius obsoletus. Biological Bulletin* **154**, 282–291.

Pechenik, J. (1979). Role of encapsulation in invertebrate life histories. *American Naturalist* **114**, 859–870. doi:10.1086/283533

Pechenik, J. A. (1982). Ability of some gastropod egg capsules to protect against low-salinity stress. *Journal of Experimental Marine Biology and Ecology* **63**, 195–208. doi:10.1016/0022-0981(82)90178-2

Pechenik, J. A. (1983). Egg capsules of *Nucella lapillus* (L.) protect against low-salinity stress. *Journal of Experimental Marine Biology and Ecology* **71**, 165–179. doi:10.1016/0022-0981(93)90071-U

Pechenik, J. A., Chang, S. C., and Lord, A. (1984). Encapsulated development of the marine Prosobranch gastropod *Nucella lapillus*. *Marine Biology* **78**, 223–229.

Pechenik, J. A., Marsden, I. D., and Pechenik, O. (2003). Effects of temperature, salinity, and air exposure on development of the estuarine pulmonate gastropod *Amphibola crenata*. *Journal of Experimental Marine Biology and Ecology* **292**, 159–176. doi:10.1016/S0022-0981(03)00159-X

Pilkington, M. (1974). The eggs and hatching of some New Zealand prosobranch molluscs. *Journal of the Royal Society of New Zealand* **4**, 411–431.

Pinder, A., and Friet, S. (1994). Oxygen transport in egg masses of the amphibians *Rana sylvatic* and *Ambystoma maculatum*: convection, diffusion and oxygen production by algae. *Journal of Experimental Biology* **197**, 17–30.

Podolsky, R. D. (2000). Intertidal embryos: temperature tradeoffs during early development. *American Naturalist* **40**, 1174.

Podolsky, R. D., and Hoffmann, G. E. (1998). Embryo development during tide-related thermal stress, evidence of a protective role for heat-shock proteins. *American Naturalist* **38**, 186.

Przeslawski, R., Davis, A., and Benkendorff, K. (2004). Effects of ultraviolet radiation and visible light on the development of encapsulated molluscan embryos. *Marine Ecology Progress Series*, **268**, 151–160.

Rawlings, T. (1990). Associations between egg capsule morphology and predation among populations of the marine gastropod, *Nucella emarginata*. *Biological Bulletin* **179**, 312–325.

Rawlings, T. (1996). Shields against ultraviolet radiation: an additional protective role for the egg capsules of benthic marine gastropods. *Marine Ecology Progress Series* **136**, 81–95.

Rawlings, T. (1999). Adaptations to physical stresses in the intertidal zone: the egg capsules of neogastropod molluscs. *American Zoologist* **39**, 230–243.

Richmond, C. E., and Woodin, S. A. (1996). Short-term fluctuations in salinity: effects on planktonic invertebrate larvae. *Marine Ecology Progress Series* **133**, 167–177.

Rodriguez, G., Ogawa, J., and Martinez-Palacios, C. (1991). Hatching of the queen conch *Strombus gigas* L. *Aquaculture and Fisheries Management* **22**, 7–14.

Roller, R., and Stickle, W. (1989). Temperature and salinity effects on the intracapsular development, metabolic rates, and survival to hatching of *Thais haemastoma canuliculata* (Gray) (Prosobrancia: Muricidae) under laboratory conditions. *Journal of Experimental Marine Biology and Ecology* **125**, 235–251. doi:10.1016/0022-0981(89)90099-3

Rose, R. A. (1985). The spawn and development of 29 NSW Opisthobranchs. *Proceedings of the Linnean Society of New South Wales* **108**, 23–36.

Rose, R. A. (1986). Direct development in *Rostanga arbutus* (Angas) (Mollusca: Nudibranchia) and the effects of temperature and salinity on embryos reared in the laboratory. *Journal of the Malacological Society of Australasia* **7**, 141–154.

Rothlisberg, P. C. (1979). Combined effects of temperature and salinity on the survival and growth of the larvae of *Pandalus jordani* (Decapoda: Pandalidae). *Marine Biology* **54**, 125–134.

Rumrill, S. (1990). Natural mortality of marine invertebrate larvae. *Ophelia* **32**, 163–198.

Sabo, M., Frederick, R., and Kelso, W. (1999). Hydrology and aquatic habitat characteristics of a riverine swamp. I. Influence of flow on water temperature and chemistry. *Regulated Rivers Research & Management* **15**, 505–523.

Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science* **283**, 2095–2097. doi:10.1126/SCIENCE.283.5410.2095

Scheltema, R. (1965). The relationship of salinity to larval survival and development of *Nassarius obsoletus* (Gastropoda). *Biological Bulletin* **129**, 340–354.

Scheltema, R. S. (1967). The relationship of temperature to the larval development of *Nassarius obsoletus* (Gastropoda). *Biological Bulletin* **132**, 253–265.

Shick, J. M., and Dunlap, W. C. (2002). Mycosporine-like amino acids and related gadusols: biosynthesis, accumulation, and UV-protective functions in aquatic organisms. *Annual Review of Physiology* **64**, 223–262. doi:10.1146/ANNUREV.PHYSIOL.64.081501.155802

Shick, J. M., Romaine-Lioud, S., Ferrier-Pages, C., and Gattuso, J. (1999). Ultraviolet-B radiation stimulates shikimate pathway-dependent accumulation of mycosporine-like amino acids in the coral *Stylophora pistillata* despite decreases in its population of symbiotic dinoflagellates. *Limnology and Oceanography* **44**, 1667–1682.

Shooter, D., Davies-Colley, R. J., and Kirk, J. T. O. (1998). Light absorption and scattering by ocean waters in the vicinity of Chatham Rise, South Pacific Ocean. *Marine and Freshwater Research* **49**, 455–461.

Smith, B., Black, J. H., and Shepard, S. A. (1989). Molluscan egg masses and capsules. In 'Marine Invertebrates of Southern Australia, Part 2'. (Eds S. Shepard and I. Thomas.) pp. 841–891. (South Australia Government Printing Division: Adelaide, Australia.)

Spight, T. M. (1975). Factors extending gastropod embryonic development and their selective cost. *Oecologia* **21**, 1–16.

Spight, T. M. (1977). Do intertidal snails spawn in the right places? *Evolution* **31**, 682–691.

Stochaj, W. R., Dunlap, W. C., and Shick, J. M. (1994). Two new UV-absorbing mycosporine-like amino acids from the sea anemone *Anthopleura elegantissima* and the effects of zooxanthellae and spectral irradiance on chemical composition and content. *Marine Biology* **118**, 149–156.

Strathmann, M. F. (1987). 'Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast.' (University of Washington Press: Seattle, WA, USA.)

Strathmann, R. (1977). Egg size, larval development, and juvenile size in benthic marine invertebrates. *American Naturalist* **111**, 373–376. doi:10.1086/283168

Strathmann, R. (1985). Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* **16**, 339–361. doi:10.1146/ANNUREV.ES.16.110185.002011

Strathmann, R. (2000). Form, function, and embryonic migration in large gelatinous egg masses of arenicolid worms. *Invertebrate Biology* **119**, 319–328.

Strathmann, R., and Chaffee, C. (1984). Constraints on egg masses 2. Effect of spacing size and number of eggs on ventilation of masses of embryos in jelly adherent groups or thin-walled capsules. *Journal of Experimental Marine Biology and Ecology* **84**, 85–94. doi:10.1016/0022-0981(84)90232-6

Strathmann, R., and Hess, H. C. (1999). Two designs of marine egg masses and their divergent consequences for oxygen supply and desiccation in air. *American Zoologist* **39**, 253–260.

Strathmann, R., and Strathmann, M. F. (1995). Oxygen supply and limits on aggregation of embryos. *Journal of the Marine Biological Association of the United Kingdom* **75**, 413–428.

Struhsaker, J., and Costlow, J. Jr. (1969). Some environmental effects on the larval development of *Littorina picta* (Mesogastropoda), reared in the laboratory. *Malacologia* **9**, 403–419.

Sullivan, C., and Bonar, D. (1985). Hatching of *Ilyanassa obsolete* embryos: degradation of the egg capsule plug in the absence of detectable proteolysis of the major plug proteins. *Biological Bulletin* **169**, 365–376.

Switzer-Dunlap, M., and Hadfield, M. G. (1977). Observations on development, larval growth and metamorphosis of four species of Aplysiidae (Gastropoda: Opisthobranchia) in laboratory culture. *Journal of Experimental Marine Biology and Ecology* **29**, 245–261. doi:10.1016/0022-0981(77)90069-7

Tamarin, A., and Carriker, M. (1967). The egg capsule of the Muricid gastropod *Urosalpinx cinerea*: An integrated study of the wall by ordinary light, polarized light, and electron microscopy. *Journal of Ultrastructure Research* **21**, 26–40.

Thompson, T. E. (1958). The influence of temperature on spawning in *Aldaria proxima* (A. and H.) (Gastropoda: Nudibranchia). *Oikos* **9**, 246–252.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* **25**, 1–45.

Williams, L. G. (1980). Development and feeding of larvae of the nudibranch gastropods *Hermissenda crassicornis* and *Aeolidia papillosa*. *Malacologica* **20**, 99–116.

Williamson, C., Hargreaves, B., Orr, P., and Lovera, P. (1999). Does UV play a role in changes in predation and zooplankton community structure in acidified lakes? *Limnology and Oceanography* **44**, 774–783.

Wissmann, S. M. (2003). The effects of elevated ultraviolet B radiation and elevated water temperature on the loss of zooxanthellae from *Aiptasia pallida*. *Transactions of the Kansas Academy of Science* **106**, 92–98.

Woods, A. (1999). Egg-mass size and cell size: effects of temperature on oxygen distribution. *American Zoologist* **39**, 244–252.

Woods, H. A., and DeSilets, R. Jr. (1997). Egg-mass gel of *Melanochlamys diomedea* (Bergh) protects embryos from low salinity. *Biological Bulletin* **193**, 341–349.

Wood, W. F. (1987). Effect of solar ultra-violet radiation on the kelp *Ecklonia radiata*. *Marine Biology* **96**, 143–150.

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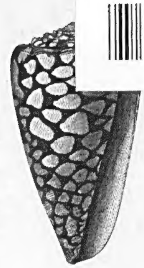

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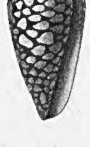

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